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EVOLUTION OF THE SILURIAN AND DEVONIAN GRAPTOLOIDS

R. B. RICKARDS
J. E. HUTT
AND
W. B. N. BERRY

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EVOLUTION OF THE SILURIAN AND DEVONIAN GRAPTOLOIDS

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EVOLUTION OF THE SILURIAN AND DEVONIAN GRAPTOLOIDS

By R. B. RICKARDS, J. E. HUTT & W. B. N. BERRY

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ABSTRACT

The evolution of the whole of the Silurian and Devonian graptoloids, that is about one-quarter of known graptolites, is discussed. For the most part actual specific lineages are described, whilst in section II *major* evolutionary concepts are only outlined on the broad evolutionary framework. A synopsis of Silurian 'trends' is given in section VI, and the extensive systematic notes (section VII) are a necessary result of the authors' investigations of the numerous groups and genera: no new taxa are proposed at the higher classificatory levels, but at generic and specific level considerable redefinition (e.g. *Atavograptus* Rickards, *Lagarograptus* Obut & Sobolevskaya) and description of newly recorded structures are required. *Atavograptus praestrachani* sp. nov. is described, and *Monograptus walkerae* nom. nov. is proposed for *M. toernquisti* Sudbury *non* Eisel.

We interpret that all monograptid evolution stems from the *atavus* group (*Atavograptus*), and almost the whole of the post-Wenlock evolution from a pristiograptid stock. Each of these evolutionary explosions follows a period of near-extinction of the graptoloids. The origins of *Pristiograptus*, *Monoclimacis* and *Monograptus* (restricted) are considered to be firmly established herein, but a lack of recent research on some groups ('*Spirograptus*', '*Globosograptus*') defines some of the problem areas. A probable polyphyletic origin of a number of groups is proposed (*Monograptus*, *Retiolites*, *Climacograptus*). Some of the detailed morphological information accumulated, together with stratigraphical occurrences, has implication concerning the mode of life of the graptoloids, but this latter topic is considered beyond the scope of the present work and is largely ignored.

I. INTRODUCTION

NOT SINCE Elles' (1922) work on the graptolite faunas of the British Isles has a comprehensive study been made of the evolution of the Silurian graptoloids. Elles devoted a good deal of her effort in that paper to the Ordovician graptoloids, but the accumulation of data on the Silurian graptoloids during the past fifty years, and in particular during the last decade, today precludes such an all-embracing study. The actual lineages which Elles proposed as a framework to the plexus of Silurian graptoloids are summarized in the last table of her paper (1922 : 200). The present paper supports only about one-third of these lineages (e.g. the *crenularis–vomerina* line) which were erected mostly upon an understanding of the silhouettes of the graptoloid species. Those suggested lineages which most modern workers would readily support (e.g. the *triangulatus–longispinus* line, redefined by Sudbury, 1958) were those which Elles erected after study of pyritized three-dimensional specimens, the next best form of preservation to isolated or transparent material. In fact the main changes in the present understanding of the evolutionaty lineages result as much from the access the writers have had to isolated and good three-dimensional material, as from the more refined stratigraphical studies of the last few years. Papers relevant to the last category include Rickards (1965, 1967, 1969, 1970), Burgess *et al.* (1970), Toghill (1968a, b), Teller (1964, 1969), Warren (1971), Koren' (1973), and Hutt & Rickards (1970).

Apart from this broadly based work of Elles there were important papers by Bulman (1958, 1963) similarly wide in scope, but not dealing with actual lineages, and in addition a number of papers on the detailed evolution of particular groups (Sudbury 1958, Urbanek 1966, 1970 etc.) : these are discussed at appropriate points in the text below, both in section II on the broad evolutionary framework and in sections III–V on the detailed evolution.

The work on which the present paper is based started about 1966 independently in Berkeley, California, where one of us (W. B. N. B.) began constructing an evolutionary lineage diagram embracing Silurian and Devonian graptoloids, and at the British Museum (Natural History) where R. B. R. developed a similar diagram, based upon geological range and species abundance, during the research training of Miss J. E. Hutt. These diagrams, essentially sketchy at first, became refined as work on the various lineages progressed, and are included here as Fig. 1. It provides a basis for discussion or investigation of the evolution of any of the groups or genera. The construction of Fig. 1 is outlined below.

A. *Range in time of a group or genus.* In one sense the diagram could only be constructed after research had decided on the composition of a group : in practice the diagram has itself evolved since it has provided ideas. The stratigraphical occurrence of each of the species in a group or genus (represented by the 'balloons') is plotted against the zonal scheme to the left of the chart. Thus *Lagarograptus* is considered to range from the *acinaces* to *sedgwickii* Zones inclusive. The zonal scheme used is largely that adopted by Cocks *et al.* (1971) for pre-Pridoli strata, and also that used in Czechoslovakia (Bouček, personal communication) and Poland (Teller 1969) for post-Ludlow strata. Occasionally, where greater precision is not possible, reference of a species may be to a grosser zone such as the *gregarius* Zone *sensu* Elles & Wood (1901–18). The range in time of graptoloid species is considered on a *world-wide basis* and the writers have used all the means at their disposal to obtain a thoroughly international coverage of the literature and actual collections. Consequently some of the generic ranges may appear to be longer than one would expect from a perusal of the British literature only, but such information

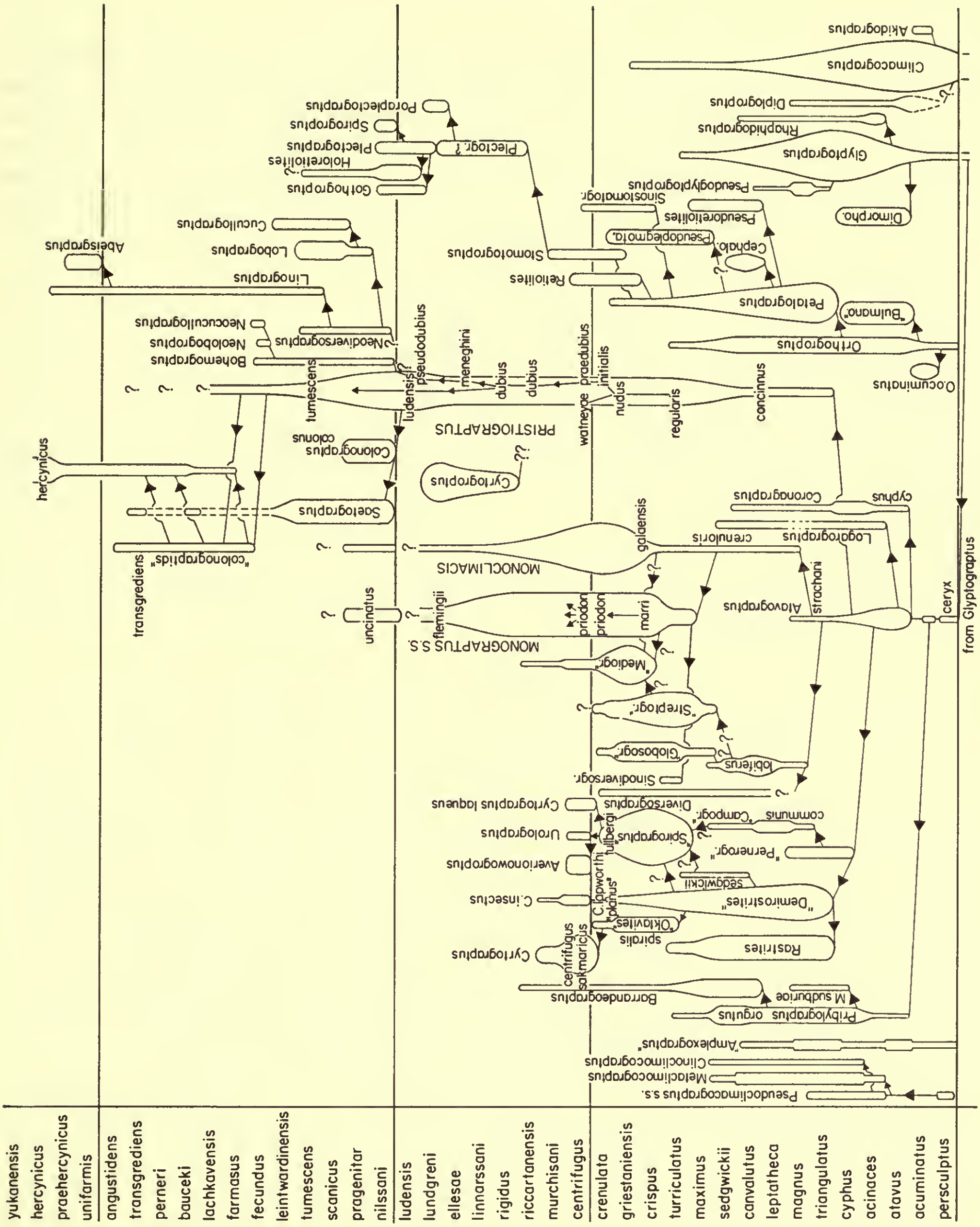

Akidograptus
Climacograptus
Diplograptus
Rhaphidograptus
Glyptograptus
Dimorpho.
Pseudoglyptograptus
Sinostomatogr.
Pseudoretiolites
Cephalo.
Pseudoplegmato.
Stomatograptus
Retiolites
Petalograptus
"Bulmano."
Orthograptus
O.acuminatus
Paraplectograptus
Spirograptus
Plectograptus
Holoretiolites
Plectogr.?
Gothograptus
Cucullograptus
Lobograptus
Abiesgraptus
Linograptus
Neocucullograptus
Neolobograptus
Neodiversograptus
Bohemograptus
hercynicus
tumescens
ludensis
pseudodubius
meneghini
dubius
dubius
praedubius
initialis
nudus
regularis
concinnus
wainwrighti
PRISTIOGRAPTUS
Colonograptus colonus
Cyrtograptus
Saetograptus
"colonograptus"
transgrediens
MONOCLIMACIS
galdensis
crenularis
Lagarograptus
Coronograptus
cyphus
uncinatus
flemingii
priodon
priodon
marri
MONOGRAPTUS S.S.
Atavograptus
strachani
ceryx
from Glyptograptus
"Mediogr."
"Streptogr."
"Globosogr."
lobiferus
Sinodiversogr.
Diversograptus
Cyrtograptus laqueus
"Campogr."
communis
Urolograptus
tullbergi
"Spirograptus"
Averianowograptus
"Pernerogr."
sedgwickii
C.lapworthi
"planus"
C.insectus
"Demirastrites"
"Oktavites"
centrifugus
sakmaricus
spiralis
Cyrtograptus
Rastrites
Barrandeograptus
M.sudburiae
Pribylograptus argutus
"Amplexograptus"
Clinoclimacograptus
Metaclimacograptus
Pseudoclimacograptus s.s.
yukonensis
hercynicus
praehercynicus
uniformis
angustidens
transgrediens
perneri
bouceki
lochkovensis
formosus
fecundus
leintwardinensis
tumescens
scanicus
progenitor
nilssoni
ludensis
lundgreni
ellesae
linnarssoni
rigidus
riccartonensis
murchisoni
centrifugus
crenulata
griestoniensis
crispus
turriculatus
maximus
sedgwickii
convolutus
leptotheca
magnus
triangulatus
cyphus
acinaces
atavus
acuminatus
persculptus

FIG. 1. Major features in the evolution of the Silurian and Devonian graptoloids. Each 'balloon' is expanded in the text and following figures. The 'standard' scheme of zones is for the purposes of this paper only, and is largely based upon Cocks *et al.* (1971), Bouček (personal communication), Jaeger (1971, personal communication) and Teller (1969). The horizontal axis indicates the approximate number of species belonging to each 'balloon' at each zone: thus the genus *Lagarograptus* is represented by one species at each successive horizon. In some cases (e.g. '*Spirograptus*') the width of the 'balloon' is necessarily approximate and has been rounded off. Some lineages are given in simplified form for direct comparison with Elles (1922).

is vital to an evolutionary understanding of the Graptoloidea. Naturally a considerable number of decisions have had to be made by the writers on the actual horizon of a species in terms of the 'standard' zonal scheme used, but it is their opinion that these decisions are themselves of great value. A drawback of such a composite chart is that some of the 'balloons' might be shown as more elongated than they should be, but where there is real doubt in the writers' minds, about either the horizon or generic assignation, they have tried to indicate this by judicious use of question marks and dashed lines.

B. *Species abundance.* The horizontal axis of the chart records the number of species recognized by the writers at any one zonal level. Thus *Lagarograptus* is represented by only one species at each zonal level or, where the lines are dashed, by lack of a record. Only in a few cases of dubious groupings ('*Spirograptus*' and '*Globosograptus*') are the 'balloons' smoothed out and approximate. In many cases the actual justification for the width of a 'balloon' is discussed in the appropriate section. For example, the *Diplograptus* occurrence is dealt with species by species in section III.3 (p. 16).

C. *Lineages.* A few lineages and 'key' species are located on the chart, particularly those forms mentioned by Elles (1922 : 200) in the same context so that a direct comparison is possible. The main text of sections III–V deals in detail with these lineages.

Therefore, in spite of the obvious drawbacks to such a diagram (its subjectivity at various levels), the writers have found it a useful basis for discussion. It is immediately obvious that *Holoretiolites*, for example, cannot on present evidence give rise to the first gothograptids, and that dimorphograptids cannot give rise to the first monograptids : other tempting morphological derivations are similarly unavailable.

Sections III–V, then, expand the framework provided by Fig. 1. It should be emphasized that these sections are not merely reviews of previous work, but include a great deal of new information based upon our own investigations. This is particularly the case in the Llandovery and Wenlock Series, but applies also to a degree to post-Wenlock evolution. The work of Sudbury (1958) and of Urbanek (1966, 1970 etc.) is treated in relation to the whole and is, naturally, synoptic. However, throughout the rest of the text, the diagrams are original and the source of the information is quoted in those few instances where it is necessary.

By examining the evolution of the whole of the Graptoloidea it is possible to define certain areas in need of considerable revision or original work, and these are indicated at the appropriate points in the text in sections III–V. The writers have made a considerable effort to see the actual material upon which the evolutionary story depends. For example W. B. N. B. and R. B. R. were fortunate to be able to study Urbanek's (1966, 1970) collections at a time when that author was actively working on them, and, with the assistance of Professor Obut and Dr Koren', to examine almost all the Russian collections monographed, including the early studies of Averianow (1929) and Levina (1928).

A very brief review of this work has appeared in section 7 of the Montreal Congress (Hutt, Berry & Rickards 1972) whilst talks on various aspects of it, usually accompanied by abstracts, have been given at the Palaeontological Association (Rickards & Hutt 1970), at the Geological Society of America (Berry 1969) and again at the Montreal Congress (Hutt *et al.* 1972, Abstracts : 226–7). The present authorship is of interest only in one further respect : in the early stages of the work there was a good deal of testy debate about who was responsible for which discovery, and it was decided that rather than spend the next decade or two in controversy the writers would join forces. The present manuscript was prepared in total by one of us (R. B. R.) and then assessed and criticized by the other two.

TEXT-FIGURES. The 'standard' zonal scheme used for the purposes of this paper is shown on the left of Fig. 1, while slightly more elaborated versions of the upper part, based largely on Polish research, are used in some diagrams such as Fig. 31. On each evolutionary diagram the known range of the species in time is indicated, in most cases by means of elongate rectangles : where the incoming and last occurrences of the species are somewhat doubtful the rectangle is broken into shorter fragments, and where there is real doubt about the occurrence we have put question marks in the appropriate positions.

The arrows shown connecting these ranges indicate the direction in which we think evolution took place : again we have placed question marks in areas of doubt. Illustrations of the species are usually given against the range rectangle, but to avoid any confusion the illustration is linked to the range either by means of an a–a notation or by fine tie lines : in several diagrams neither is necessary.

In general the illustrations are drawn from actual specimens, but where drawn from previous illustrations they have almost always been redrawn. In a few instances some idealized drawings have been included (e.g. Fig. 17).

We have attempted throughout to give magnifications and to keep all the magnifications on one figure the same, but sometimes, such as on the chart of the evolution of the cyrtograptids (Fig. 42), this has proved impracticable. However, magnifications are given in the figure explanations, as are the specimen numbers and depositories of the specimens, so that the illustrations can be checked directly.

ACKNOWLEDGEMENTS. We should like to thank collectively many colleagues throughout the world who have helped with loan of specimens and with information, often unpublished, relating to stratigraphy. Specimen depositories are indicated as follows : BM(NH), British Museum (Natural History), London ; SM, Sedgwick Museum, Cambridge ; LO, Lund University ; LU, Leicester University ; GSM, Geological Survey Museum (Institute of Geological Sciences) ; BU, Birmingham University ; HUR, Hull University Department of Geology, Rickards Collection ; AMNH, American Museum of Natural History ; USNM, United States National Museum ; TCD, Trinity College, Dublin.

II. GENERAL EVOLUTIONARY FRAMEWORK

George (1962 : 41) considered thecal elaboration in graptolites a cladogenetic divergence, implying that major rhabdosomal changes involved anagenesis. In discussing the graptoloids Bulman (1963 : 407) took a similar view and defined the following anagenetic grades in more or less ascending stratigraphic order: 1, multiramous; 2, tetragraptid; 3, didymograptid; 4, diplograptid; 5, monograptid. Cladogenetic divergence was exemplified in this last work by leptograptid and dicellograptid production from grade 3, by retiolitid, lasiograptid and glossograptid production from grade 4 and by 'dimorphograptid' production from grade 5. In stratigraphic terms grade 4 survives into the Silurian and grade 5 is typically Silurian. The present writers, therefore, in discussing the evolution of Silurian graptoloids, are dealing broadly with cladogenetic divergence, but also with the anagenetic change in grade from diplograptid to monograptid (sections 4, 5, 6, 8, 9, 11, 12 and 13 below).

Bulman (1963 : 401) remained cautious, however, in applying Huxley's (1958) grades and ensuing cladogenesis to colonial organisms, pointing out (p. 402) that '. . . in any non-colonial group of organisms thecal characters would necessarily represent the natural and only basis for classification'. Changes in *rhabdosomal* form are almost always abrupt and discontinuous, for example an increase in length of the uniserial portion of the dimorphograptid stipe is extremely rare if not doubtful (Rickards 1963, 1970). George (1962 : 41) considered thecal elaboration '. . . scarcely to be regarded as a "trend" (if the word is to contain as an element of its meaning a hint of channelled direction of limited variability) ; and most of the lineages are broadly monophyletic especially in the prolific diversity of early Silurian faunas'. We feel that the evidence of lineages and thecal elaboration described below tends to contradict this opinion, and would urge caution in applying the cladogenesis/anagenesis concept too rigidly.

For the most part, however, we outline below actual lineages of species, or suggested lineages and suggested problem areas, and avoid for the present major evolutionary concepts. Examination of Fig. 1, the construction of which was explained above (p. 6), shows that the Silurian and Devonian graptoloids enjoy two genuine evolutionary 'bursts' and suffered two crippling evolutionary 'lows' before extinction probably in the Emsian. Reasons for these 'lows' and 'bursts' are not discussed here, since at best our ideas are speculative, but it may be noted that both evolutionary expansions coincide with marked transgressions in the northern hemisphere, whilst the Ashgill 'low' is coeval with the strange Hirnantia fauna which is possibly a cold water fauna developed during glaciation in Africa and South America (Berry & Boucot 1972). One of the main aims of this work has been the actual definition of such 'lows' in terms of the evolutionary lineages. Of the two evolutionary expansions, in the Llandovery and the Ludlow, that in the Llandovery involves the establishment of some thirty genera or 'groups' from about ten to fifteen species or subspecies belonging to five or six genera in the Ashgill Series of the Ordovician : the actual origins of these groups are suggested. In the Ludlow expansion some fifteen 'genera' evolve from a very limited number of late Wenlock pristiograptids : the survival into the Ludlow of hooked monograptids of the *priodon* type such as *M. uncinatus* is difficult to explain in view of their apparent absence in much of the *ludensis* Zone and *nassa–dubius* interregnum (*nassa* Zone of some authors). An extra-geosynclinal oceanic source of much of the plankton is possible ; whilst this might explain the absence of such forms at the top of the Wenlock the mechanism would not be required elsewhere for an evolutionary story in which most of the chapters seem to be present. Rather, it is probably more correct to suppose that the whole Wenlock period represented a period of waning or at least stagnating graptolite evolution and that hooked monograptids became extremely rare, almost extinct, near its end : Ludlow monoclimacids may well have evolved independently from pristiograptids (p. 55 below) and not from *M. flumendosae,* the only *lundgreni* Zone monoclimacid known. Warren (1971) may, therefore, be correct in recording *M.* aff. *uncinatus orbatus* from the top of the *ludensis* Zone recognized in north Wales. Such rare occurrences in future studies might be predicted.

Evolutionary studies of Silurian and Devonian graptoloids have mostly been concerned with particular groups (e.g. Sudbury 1958) and these are discussed in the appropriate sections below. Papers of a more general synoptic nature have been attempted, such as Bulman's (1958, 1963) outlines of the evolution of the whole of the Graptoloidea including Ordovician groups. Elles' (1922) paper had a similar coverage but proposed actual lineages linking successive genera or groups. Since Elles' work the degree of refinement of both the Silurian stratigraphy and palaeontology has been considerable, and we can redefine her lineages and suggest many more based upon our own research. Essentially, however, the present account of the evolution of the Silurian and Devonian graptoloids may be regarded as an extension of Elles' approach, with more than half a century of additional information, rather than a paper of synoptic kind.

III. ORDOVICIAN REMNANTS

1. '*Amplexograptus*' and the *Climacograptus innotatus* group. *Climacograptus innotatus* Nicholson was placed in the genus *Amplexograptus* by Lee (1963) on the grounds that the supragenicular wall is short and almost vertical, and the thecal excavations long and semicircular. The nature of the characteristic genicular 'spines' (Fig. 2) was not ascertained, but subsequently Stein (*in* Wolfart *et al.* 1968) interpreted these processes as genicular hoods. This is in accord with our own less sophisticated observations on this species which suggest that the Silurian forms of *C. innotatus* have a single, genicular, probably hood-like structure on each thecal tube. The following subspecies have been recognized to date :

Silurian
C. i. innotatus Nicholson ; *acuminatus–gregarius* Zones
C. i. exquisitus Rickards ; *atavus* Zone
C. i. jordaniensis Stein ; *gregarius–convolutus* Zones
C. i. braziliensis Ruedemann
C. i. obesus Churkin & Carter ; *cyphus* Zone (= *C. i. innotatus*)

Ordovician
C. i. subsp. undescribed ; Ruedemann 1947 : 428 ; highest Ordovician
C. i. pacificus Ruedemann ; highest Ordovician
C. i. occidentalis Ruedemann ; Fairmount Beds (? = *C. manitoulinensis* Caley)
C. i. nevadensis Carter ; approximately *linearis* Zone

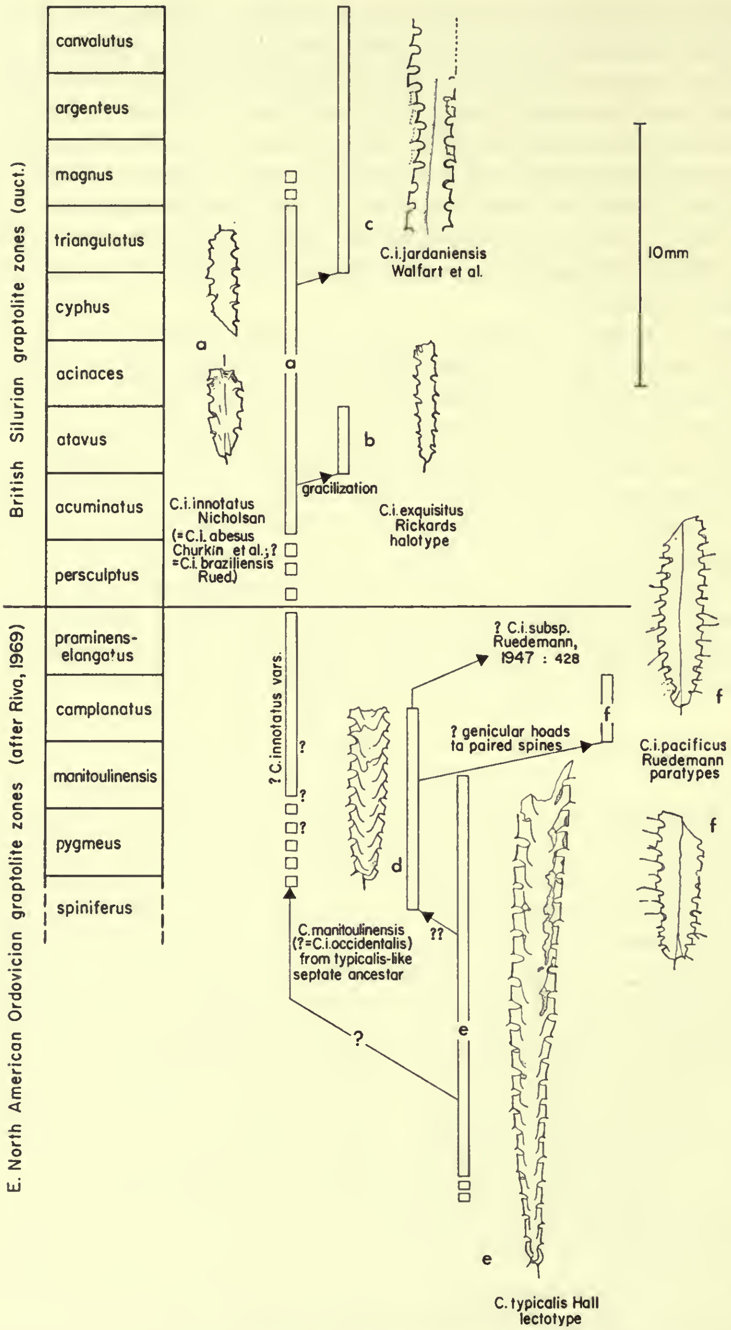

British Silurian graptolite zones (auct.)
convolutus
argenteus
magnus
triangulatus
cyphus
acinaces
atavus
acuminatus
persculptus
E. North American Ordovician graptolite zones (after Riva, 1969)
prominens-elongatus
complanatus
manitoulinensis
pygmeus
spiniferus
a
a
C.i.innotatus Nicholson
(=C.i. obesus Churkin et al.;? =C.i. braziliensis Rued.)
c
C.i.jardaniensis Walfart et al.
10mm
b
gracilization
C.i.exquisitus Rickards holotype
? C.innotatus vars.
?
?
?
? C.i.subsp. Ruedemann, 1947 : 428
? genicular hoods ta paired spines
f
f
f
C.i.pacificus Ruedemann paratypes
d
??
C.manitoulinensis (?=C.i.occidentalis) from typicalis-like septate ancestar
?
e
e
C.typicalis Hall lectotype

Fig. 2. Evolution of the *C. innotatus* group of species: a, LU 4019 and LU 4018; b, HUR 1Bi/126; c, after Wolfart *et al.* (1968); d, Riva Collection; e, AMNH 1090; f, USNM 1368 and unnumbered paratype. × 3½.

The Silurian forms are mostly low Llandovery in age, and are best considered to have evolved directly from similarly specialized upper Ordovician species. *C. innotatus* itself, however, has been recorded as low as the *clingani* Zone (Churkin 1963 ; Churkin & Kay 1967) but there must be considerable doubt whether this is the same form : confusion with *C. manitoulinensis* or *C. i. pacificus* (Fig. 2) would be all too easy. The type material of *C. i. pacificus*, however, possibly exhibits paired genicular spines and probably not, as figured by Ross & Berry 1963 (Fig. 2 herein), a single genicular process ; this leaves *C. i. occidentalis* as the only likely described ancestor since genicular spines in a biserial graptolite can be considered as extremely specialized structures with little scope for morphological change to genicular hoods.

Genicular hoods are particularly common in Silurian graptolites (*Pseudoclimacograptus, Monoclimacis*), but are not restricted thereto, for similar flange-like processes are found, for example, on *C. typicalis* Hall and some of its subspecies. It is possible that the *innotatus* species group has evolved from late forms of *C. typicalis* which have themselves almost amplexograptid thecae, or perhaps more probably from a *typicalis*-like septate species. However, the reference of *C. innotatus* to *Amplexograptus* by Lee (1963) is unconvincing partly because of the complete lack of amplexograptids in the uppermost Ordovician (except, possibly, *C. inuiti* Cox) but mainly because the presence of pronounced thecal processes surely sets these forms apart from *Amplexograptus* s.s. If the existence of an amplexograptid ancestor were established there would be a case for considering *C. innotatus* and its subspecies as a subgenus of *Amplexograptus*. We think it more likely that the *C. innotatus* group has evolved from a climacograptid or climacograptids by a process which had earlier produced amplexograptids, but which at such a late date involved the development of typically Silurian structures such as genicular hoods and, for biserial graptolites, small rhabdosome size (Fig. 2).

C. innotatus Nicholson is the type species of the monotypic subgenus *Climacograptus* (*Paraclimacograptus*) Přibyl (1947), erected to include climacograptids with thecal spines throughout the length of the rhabdosome. It is now known (Wolfart *et al.* 1968) that the thecal spines *sensu* Přibyl are, in fact, genicular hoods, and whilst his attribution recognizes the affinity of *C. innotatus* with *Climacograptus* rather than *Amplexograptus* there seem no grounds for erecting a subgenus to embrace a small climacograptid with genicular hoods. It should be emphasized that while the genicular hoods of *C. innotatus* are in all probability composed of microfusellar tissue (as in *P.* (*Metaclimacograptus*) *undulatus* Kurck) this has not yet been established.

The *innotatus* group marks the end of a minor line of evolution, and the Silurian members are typically tiny, whilst the recognized subspeciation probably involves a strong geographical as opposed to temporal element. On morphological grounds their evolutionary prospects were limited, and in many respects they paralleled the Silurian development of the pseudoclimacograptids discussed below (p. 14), a group which is also best considered as an Ordovician remnant in the Silurian and which was subjected to the changes affecting many graptolites at this time (p. 84), including the formation of genicular hoods.

2. *Pseudoclimacograptus.* Silurian representatives are few and some aspects of their evolution have been briefly discussed by Bulman & Rickards (1968) who regarded *P.* (*Metaclimacograptus*) *hughesi* (Pl. 2, fig. 2), *P.* (*M.*) *undulatus* and *P.* (*Clinoclimacograptus*) *retroversus* as late offshoots of *P.* (*Pseudoclimacograptus*) (Fig. 3). As with *C. innotatus* these species developed typical Silurian features: pronounced genicular hoods, specialized median septa in *hughesi* and *undulatus* and strong apertural eversion in *retroversus*. *P. orientalis* Obut & Sobolevskaya (Fig. 3b), typical of the *cyphus* and *triangulatus* Zones in the U.S.S.R., is probably a true *P.* (*Pseudoclimacograptus*) and may provide a link with the rare late Ordovician pseudoclimacograptids (e.g. *P.* cf. *clevensis* Riva 1969). Two of us (J. E. H. &

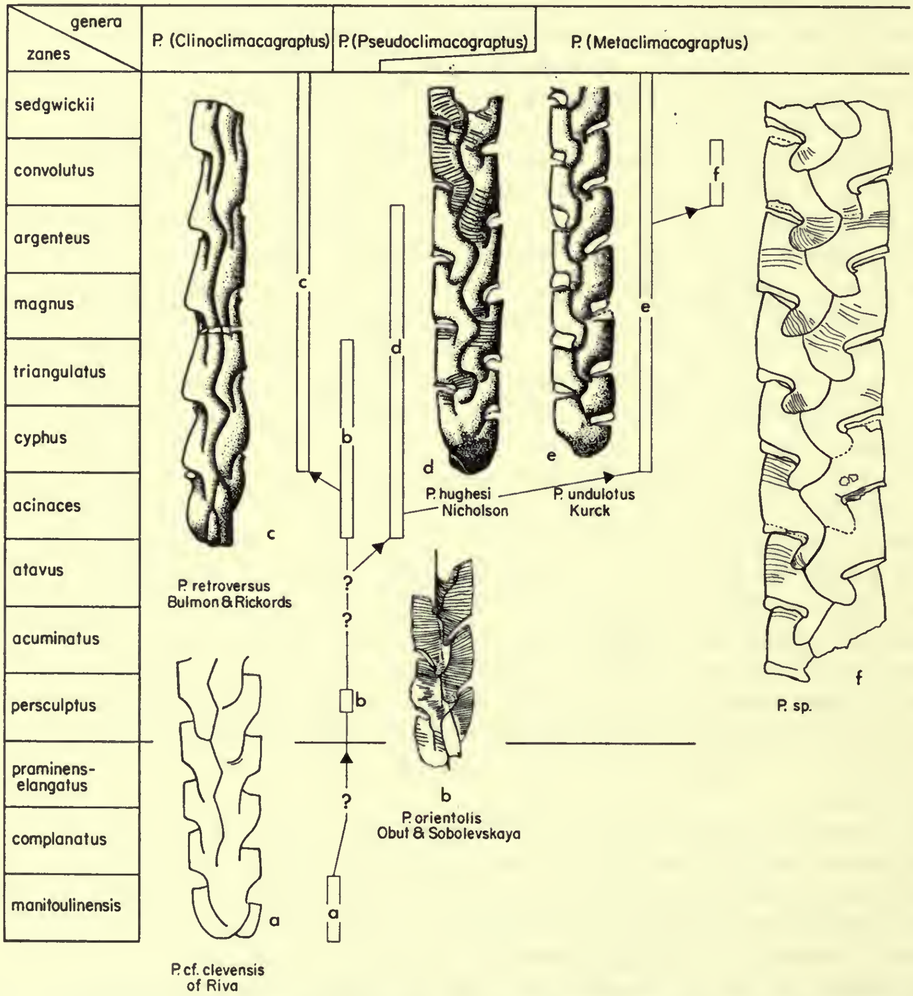

genera
zones
P. (Clinoclimacograptus)
P. (Pseudoclimacograptus)
P. (Metaclimacograptus)
sedgwickii
convolutus
argenteus
magnus
triangulatus
cyphus
acinaces
atavus
acuminatus
persculptus
praminens-elangatus
complanatus
manitoulinensis
c
b
d
e
f
a
?
?
?
P. hughesi Nicholson
P. undulotus Kurck
P. retroversus Bulman & Rickords
P. orientolis Obut & Sobolevskaya
P. sp.
P. cf. clevensis of Riva

Fig. 3. Evolution of *Pseudoclimacograptus*: a, after Riva (1969); b, SM A86379; c, GSM WEG4052; d, SM A23912; e, SM A23090; f, SM A87575. All figures × 14.

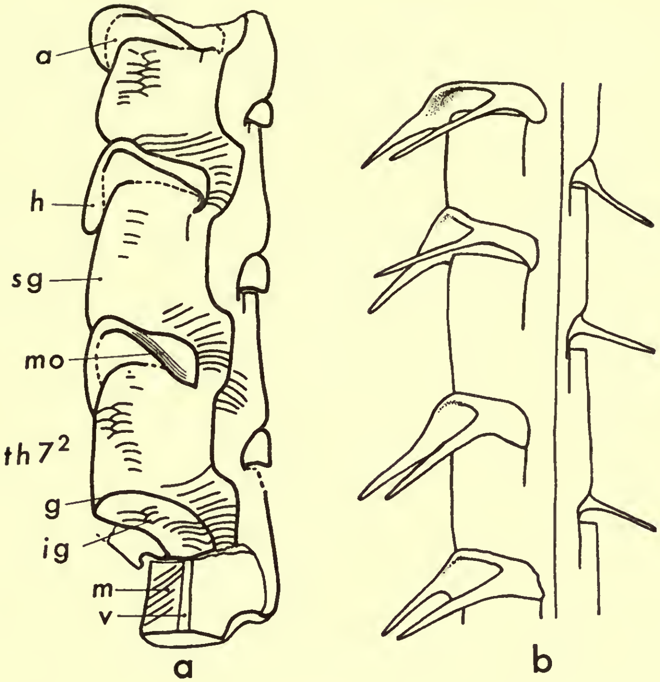


FIG. 4. a, *Pseudoclimacograptus* (*Metaclimacograptus*) *undulatus* (Kurck), SM A52953; b, hypothetical manner in which hoods of microfusellar tissue might develop paired spines. Both ×40.

R. B. R.) have recently found *P. orientalis* in the *gregarius* Zone of Dalarne, Sweden. All the Silurian members of the genus are small compared with many Ordovician forms and, except for *P. orientalis*, show distinct Silurian characters upon a basic pseudoclimacograptid pattern (Fig. 3). The last known pseudoclimacograptids occur in the *sedgwickii* Zone.

P. (*M.*) *hughesi* may be intermediate between the earlier forms of *P.* (*P.*) *orientalis* and the later *P.* (*M.*) *undulatus*. This involves the development of an angular from an undulating or zigzag median septum, and an even smaller rhabdosome (0·5 mm dorsoventral width) and very close packing of the thecal tubes: indeed the angular median septum seems designed to facilitate the close packing of thecae. The pronounced genicular hoods of microfusellar tissue (Fig. 4a) on *P.* (*M.*) *undulatus* may be more strongly developed than in *P.* (*M.*) *hughesi*. The full extent of such delicate structure is often difficult to discern: nevertheless the genicular processes in Ordovician species of *Pseudoclimacograptus* seem little more than flanges.

The development of tiny pseudoclimacograptid rhabdosomes is in accord with similar diminutive rhabdosomes of the last members of other biserial groups (*Climacograptus*, *Glyptograptus*, *Orthograptus*, *Holoretiolites*), whilst the genicular hoods effectively result in the *hooked* thecal tube which, in *Monograptus* s.l., appears at the same horizon. The first known thecal hooks possibly occur in the Ordovician *hirundo* Zone (*Atopograptus*), and definitely in post-*hirundo* strata at Port-au-Port, Newfoundland (? *Atopograptus* sp. nov., Rickards & Whittington in prep.), but in general they can be considered as Silurian morphological features which affect different groups at about the same time, beginning with *Pseudoclimacograptus* and *Monograptus* s.l. in the *cyphus* zone.

3. *Diplograptus*. This is one of the more difficult early Silurian genera to place in an evolutionary setting. Bulman (1955, 1970) points out that there is a gap in the record at the level of the highest Caradoc and most of the Ashgill ; the essentially early Silurian species have proximal thecae which are more climacograptid than amplexograptid. In the uppermost Ordovician, apart from *Diplograptus modestus* (Pl. 1, fig. 4), which has a universal acme in the Silurian, we are aware of only *Diplograptus fastigatus* Davies from the British Isles. Such rare species may be the ancestors of the Silurian species, and may also originate from the earlier *Diplograptus* s.s. species, but it seems more likely that latest Ordovician and early Silurian diplograptids had their origins in either the genera *Orthograptus* and *Glyptograptus* (by proximal introduction of new characters) or in the genus *Climacograptus* (by distal introduction of new characters). In our opinion *Glyptograptus* is the most likely ancestor : whereas *Orthograptus* is a 'waning' genus in the early Silurian, *Glyptograptus* is known to have had the potential to produce species of *Climacograptus* (Packham 1962) and other graptolite genera by increasing the sharpness of the geniculum. On the other hand, *Glyptograptus* itself becomes all but extinct in the Ashgill, being represented by very few species.

In fact, although typical of the low Silurian Zones of *persculptus* and *acuminatus* and thereafter surviving into the *magnus* Zone, there is only a small number of Silurian species of *Diplograptus* : *D. modestus* Lapworth (and subspecies *parvulus*, *tenuis*, *applicatus*), *D. diminutus* Elles & Wood (Pl. 1, fig. 6), *D. elongatus* Churkin & Carter, *D. magnus* H. Lapworth (Pl. 3, figs 1 & 5 ; Pl. 4, figs 1 & 2), *D.* ? *rarus* Rickards, *D. thuringiacus* Stein, *D. fezzanensis* Desio, *D. africanus* Legrand. We have been unable to recognize any genera with an entire periderm which may have been derived from these diplograptids, whilst relationships within the diplograptids themselves have hitherto proved impossible to unravel, although Legrand (1970) convincingly demonstrated the derivation of *D. fezzanensis*, with its almost petalograptid distal thecae, from *D. africanus*.

The Silurian diplograptids are, therefore, best regarded as a quite small group of Ordovician remnants, with low evolutionary potential, which had their origins late in the Ordovician probably through rare representatives of the genus *Glyptograptus*. It is important to add that knowledge of the group is poor, and the possibility remains that they may have originated through a genus such as *Climacograptus* with a more complex thecal type than *Glyptograptus*.

4. *Climacograptus*. Unlike *Pseudoclimacograptus* other climacograptids are well represented in the late Ordovician and early Silurian (Fig. 1), enjoy something of an expansion from the *acuminatus* to the *triangulatus* Zones, and are finally represented by a single species *Climacograptus nebula* (Toghill & Strachan) from the

upper *turriculatus* to *griestoniensis* Zones inclusive. However, Jaeger (personal communication) found a stratigraphically quite isolated occurrence of *Climacograptus* sp. from the Devonian rocks of the Carnic Alps: W. B. N. B. examined specimens of it and J. E. H. and R. B. R. have examined good photographs of the specimens in question and are quite convinced of their authenticity, but have no reasonable interpretation of its presence some 40 million years after *C. nebula*. Professor Urbanek (personal communication) informs us that some Devonian monograptid populations, in his isolated Polish material, occasionally have biserial specimens, or partly biserial specimens; thus such occurrences may represent other instances of Jaanusson's (1973) dithyrial populations (see p. 38).

C. normalis Lapworth (Pl. 2, fig. 3; Pl. 3, fig. 4) and *C. miserabilis* Elles & Wood probably both occur in the highest Ordovician rocks, together with *C. supernus*

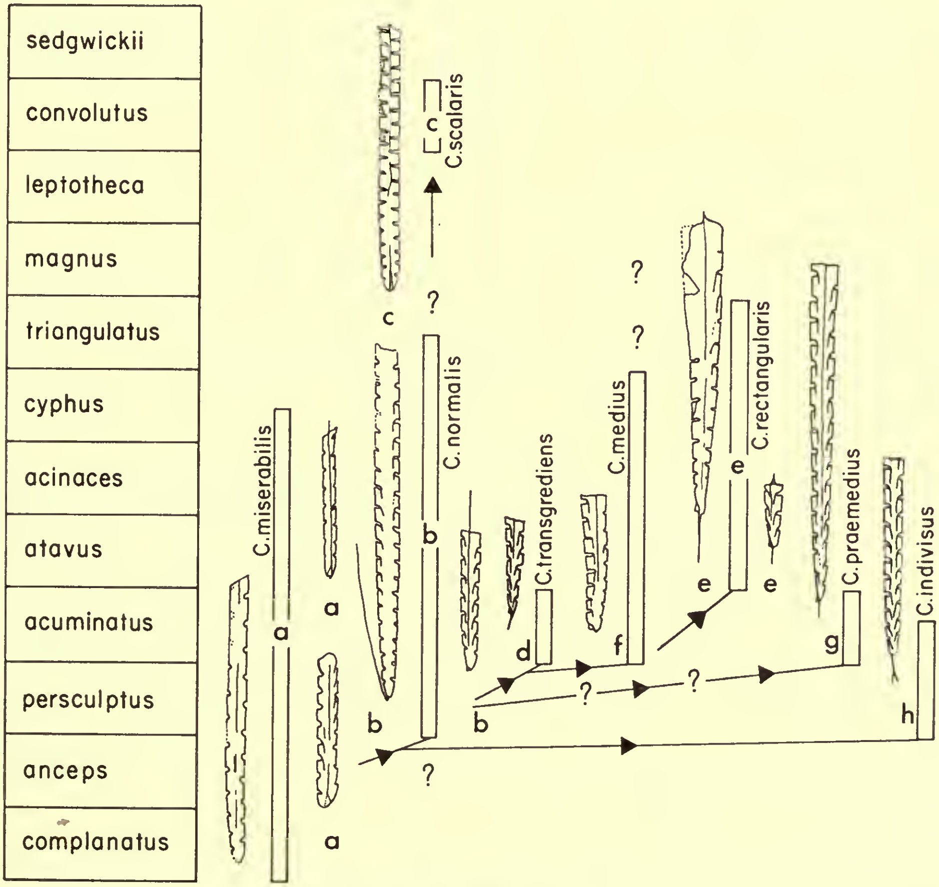

sedgwickii
convolutus
leptotheca
magnus
triangulatus
cyphus
acinaces
atavus
acuminatus
persculptus
anceps
complanatus
C.miserabilis
a
a
a
b
b
?
C.normalis
b
c
?
c
C.scalaris
C.transgrediens
d
b
C.medius
f
?
?
?
?
e
e
e
C.rectangularis
C.praemedius
g
C.indivisus
h

FIG. 5. Evolution of *Climacograptus*: a, BM(NH) Q2891, HUR S5-9/125 and BM(NH) Q2867; b, HUR 2Bi/96, and after Waern (1948); c, Riksmuseum Cn 1040; d, after Waern (1948); e, HUR S9-13/103, and after Waern (1948); f–h, after Waern (1948). All figures × 2½. [*praemedius* should read *premedius*.]

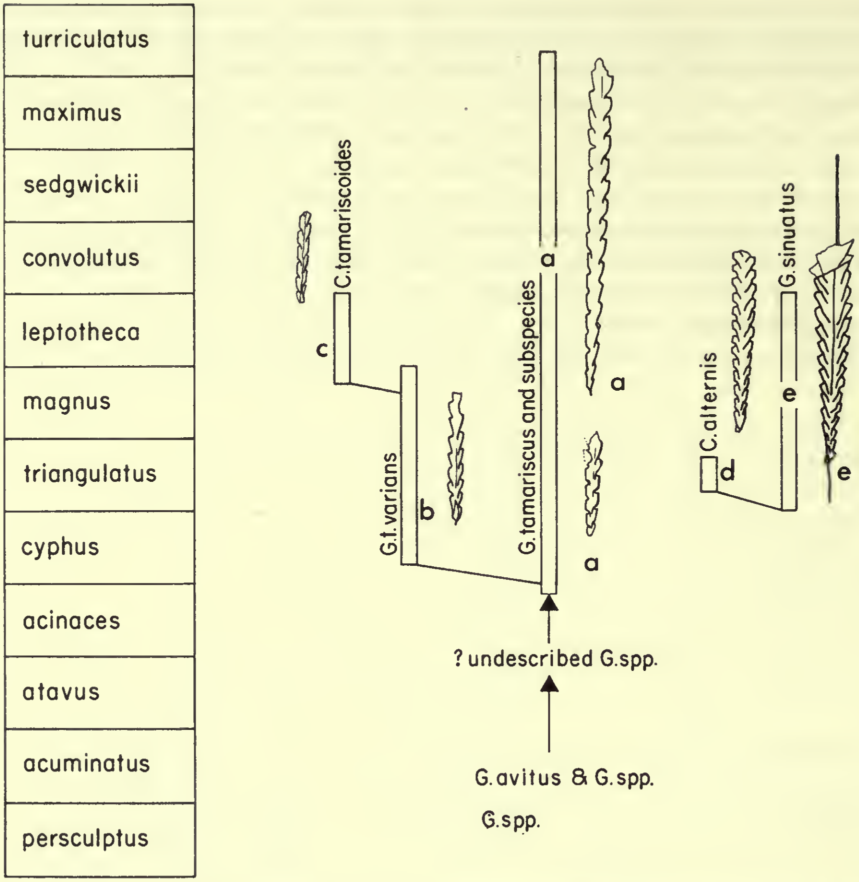

turriculatus
maximus
sedgwickii
convolutus
leptotheca
magnus
triangulatus
cyphus
acinaces
atavus
acuminatus
persculptus
C.tamariscoides
c
G.t.varians
b
G.tamariscus and subspecies
a
a
a
? undescribed G.spp.
G.avitus & G.spp.
G.spp.
C.alternis
d
G.sinuatus
e
e

Fig. 6. Evolution of *Glyptograptus* and some *Climacograptus* species from glyptograptids; a, Scottish Geological Survey 5619 and BM(NH) 24953; b, SM A51435; c, SM A24924; d, SM A24957; e, HUR 6Bi/30. All figures ×2½.

Elles & Wood, *C. latus* Elles & Wood and *C. hvalross* Ross & Berry. *C. normalis* and *C. miserabilis* persist into the Silurian and undoubtedly gave rise to a number of other species such as *C. rectangularis* McCoy, *C. medius* Törnquist (Pl. 1, fig. 5), *C. scalaris* (Hisinger), *C. premedius* Waern, *C. transgrediens* Waern and *C. indivisus* Davies. There are several other climacograptid species in the lower Llandovery indicating a sharp expansion from the four to six species typical of the highest Ordovician.

Some suggested evolutionary lineages have been published for these early Silurian climacograptids. Davies (1929) considered *C. miserabilis* to have evolved into *C. normalis* and *C. medius* (Fig. 5), whilst Waern (1948) established convincingly the lineage *C. normalis* → *C. transgrediens* → *C. medius*. In this latter line later forms have a tendency to enclose more of the sicula in the early thecae, the dorso-ventral width in general increases, the thecae become more closely spaced and the median septum is progressively delayed (Fig. 5). In addition to this line Waern thought that *C. premedius*, *C. indivisus* and *C. rectangularis* might also have been derived from *C. normalis*.

The distinction of Silurian climacograptids from glyptograptids is not always easy (Packham 1962) and usually an arbitrary distinction is made whereby the supragenicular wall in climacograptids is more or less long and vertical and the infragenicular wall inclined at more than 45° from the vertical. It is possible that evolutionary links occur between the two genera (Packham 1962 : fig. 6 ; and see Fig. 6, p. 18) and if this is correct then it implies that there are two basic groups of Silurian climacograptids : those derived from the *C. miserabilis* stock which *retain* vertical supragenicular walls, and those derived from Silurian *Glyptograptus* species such as *G. tamariscus varians* which acquire them. The latter group includes just those species in which the supragenicular wall may be not quite vertical (*C. alternis*, Fig. 6) and the infragenicular wall dubiously more steeply inclined than 45°. Thus *Climacograptus* includes species which are essentially Ordovician remnants, albeit with a Silurian expansion, and those which betray the vigour of the glyptograptid evolutionary stock in the Silurian.

IV. SILURIAN BISERIAL GRAPTOLOIDS AND DERIVATIVES

A. Groups with periderm entire

5. *Akidograptus ascensus.* Some groups in the early part of the Silurian derived from biserial graptolites are typified by protraction of the proximal regions, either by elongation of the early thecae and sicula ('*Akidograptus*') or by omission of one of the thecal series at the proximal end ('*Dimorphograptus*'). Unlike *Glyptograptus* or *Orthograptus*, from which a number of derivatives can be identified, *Climacograptus* probably gives rise only to *Akidograptus ascensus* Davies, the type species of the genus. It is characterized (Fig. 7) by distinctly climacograptid thecae and an extremely elongate sicula and thecae. No truly dimorphograptid condition is reached and the thecal sequence 1^1, 1^2, 2^1, 2^2 etc. can be recognized. Bulman (1932, 1936), however, considered that a shortened and vestigial th1^2 'seems to be present in the genotype' (1936 : 23). This, coupled with shortening of th2^2, resulted in an apparently normal sequence of thecae even though the proximal end

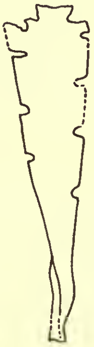


FIG. 7. *Akidograptus ascensus* Davies, LU 57528, Yewdale Beck, Lake District ; specimen somewhat broadened by compression, to show climacograptid thecae of genus. × 10.

was somewhat drawn out. Bulman (personal communication) was later less certain of this observation, but one of us (R. B. R.) has examined the type specimens and tends to support Bulman's earlier conclusions.

It is shown below that *Rhaphidograptus toernquisti* is derived from a subspecies of *Glyptograptus persculptus* and as far as we are aware there are no other akidograptids, rhaphidograptids or dimorphograptids which, because of their climacograptid-like thecae, might be supposed to originate from species of the genus *Climacograptus*.

6. *Glyptograptus*. Like *Diplograptus*, this became almost extinct in the highest Ordovician and we are aware of only *G. nicholsoni* Toghill amongst described species, although there are several undescribed, uncommon forms in both the highest Ordovician rocks (e.g. *G.* n. spp. of Riva 1969) and the *persculptus* to *acinaces* Zones in the Llandovery. There is considerable expansion of the genus in strata following the *acinaces* Zone of the Silurian, both in number of species and of specimens, but the final record seems to be that of *G.* ex gr. *fastigans* Haberfelner (Hutt, Rickards & Skevington 1970) from the *turriculatus* Zone of the upper Llandovery. We prefer to place *G. nebula* Toghill & Strachan (1970), which ranges into the *griestoniensis* Zone, in the genus *Climacograptus*. This decision does, however, exemplify a real difficulty with the Llandovery glyptograptid–climacograptid plexus: the mid-Llandovery glyptograptid expansion was studied by Packham (1962) who attempted to deduce evolutionary lineages, emphasising the (often) arbitrary distinction between *Climacograptus* and *Glyptograptus*. His decision, which has been largely followed by subsequent workers, was to place species in *Climacograptus* if the supragenicular wall was more or less vertical and the infragenicular wall inclined to the axis at an angle greater than 45°. Such a process necessitates the derivation of *C. tamariscoides* from *G. tamariscus varians* (Fig. 6) and makes Silurian climacograptids a polyphyletic group: earlier climacograptids were certainly derived from upper Ordovician ancestors of the *C. normalis* type.

Unlike *Climacograptus* and *Diplograptus* the genus *Glyptograptus* had tremendous evolutionary potential and probably gave rise to the early monograptids (Rickards & Hutt 1970) which in turn led to at least the bulk of monograptids, including *Monograptus*, *Monoclimacis* and *Pristiograptus*; see later sections. The divergence of glyptograptids began in the *cyphus* Zone (Packham 1962: fig. 6) after a *persculptus* Zone to *acinaces* Zone period where they were represented by very few species and mostly rare specimens. In the Llandovery, in addition to the *tamariscus* group and derivatives studied by Packham, were *G. s. sinuatus* (Nicholson) and its successor *G. s. crateriformis* Rickards (Figs 8d, c), *G. cuneatus* Rickards, *G. nikolayevi* Obut & Sobolevskaya, *G. tariti* Legrand and others probably also only distantly related to the *tamariscus* group. Whilst Packham was able to erect a convincing lineage for the well-represented *tamariscus* group the problem with the remaining glyptograptids is their sporadic and relatively rare occurrence. Thus *G. persculptus* (Pl. 2, fig. 4) occurs in the highest Ordovician rocks and in the *persculptus* Zone with *G.* sp. (Rickards & Hutt); the *acuminatus* Zone has *G. avitus* Davies and *G.* sp. 1 of Rickards (1970).

Packham (1962 : 523 *et seqq.*) suggested a derivation of the whole *G. tamariscus* group from *G. avitus*. Within the *tamariscus* group itself three lineages were distinguished, each leading from *G. tamariscus tamariscus*, which as forms A, B and C span the *acinaces* to *turriculatus* Zones :

1. *G. t. tamariscus* A → *G. tamariscus linearis* → *G. serratus barbatus*, involving increasingly robust rhabdosomes, probably lengthening of th1^1, and development in the end member of sicular, genicular and other thecal spines or processes.

2. *G. t. tamariscus* A → *G. t. varians* → *C. tamariscoides*, involving probable decrease in the length of th1^1, and increased geniculation to the extent that Packham places the end member of the lineage in the genus *Climacograptus*.

3. *G. t. tamariscus* A → *G. t. acutus*, involving possible decrease in the length of th1^1 and increased geniculation, but with variable thecal spacing from one member to the next.

G. s. sinuatus and *G. s. crateriformis* succeed and are similar in many respects to the *G. persculptus* plexus, and we note that *G. sinuatus* is often difficult to distinguish, in the distal regions, from *Rhaphidograptus toernquisti* (Elles & Wood) which we contend (p. 24) evolved also from a member of the *persculptus* plexus. *G. nikolayevi* (*acinaces* Zone) is a possible morphological and stratigraphical intermediate between *G. persculptus* and *G. sinuatus*, which latter appears as early as the *cyphus* Zone (Rickards 1970 : 43).

The few remaining species of Silurian glyptograptids, and the small number of undescribed species at certain horizons, are in need of considerable study before evolutionary relationships can be suggested. In succeeding sections (7–10, pp. 21–25 ; 20, pp. 36–39) the relationships of glyptograptids to other genera and subgenera are discussed.

7. *Glyptograptus* (*Pseudoglyptograptus*). The subgenus was erected by Bulman & Rickards (1968) to include glyptograptids with a pronounced concavoconvex supragenicular wall and slightly everted apertural regions (Fig. 8). Subsequent work was carried out by Rickards (1972) and Rickards & Koren' (1974) so that the subgenus is now represented by the following forms :

G. (*P.*) *vas* Bulman & Rickards ; *magnus* Zone
G. (*P.*) sp. 1 Rickards ; exact horizon not known
G. (*P.*) sp. 2 Rickards ; *magnus* Zone
G. (*P.*) *rhayaderensis* Rickards & Koren' ; *triangulatus* Zone (= *G.* (*P.*) sp. 3 Rickards)
G. (*P.*) *tabukensis* Rickards & Koren' ; *convolutus* Zone

The last two species exhibit sicular spinose bundles (Rickards & Koren' 1974) not unlike that seen in *G. serratus barbatus* and '*Comograptus*' *comatus* Obut & Sobolevskaya. Further work on three-dimensional material will be required to decide whether these species also belong in *G.* (*Pseudoglyptograptus*).

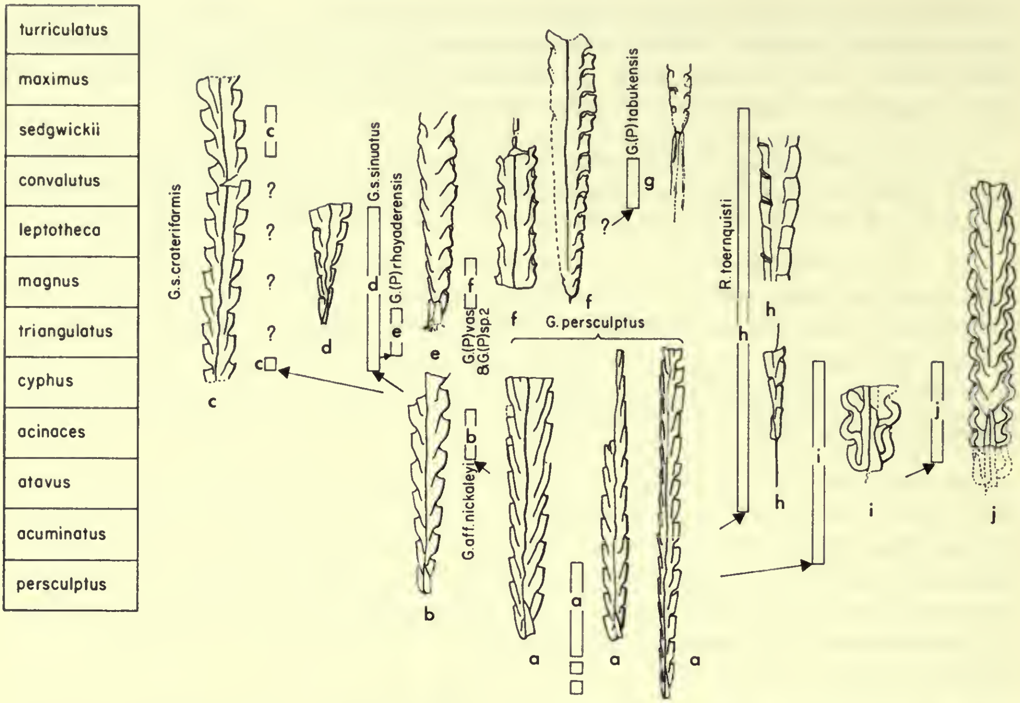

turriculatus
maximus
sedgwickii
convalutus
leptotheca
magnus
triangulatus
cyphus
acinaces
atavus
acuminatus
persculptus
G.s.crateriformis
G.s.sinuatus
G.(P.)rhayaderensis
G.(P.)vas & G.(P.)sp.2
G.aff.nickoleyi
G.(P.)tabukensis
R.toernquisti
G.persculptus
a
b
c
d
e
f
g
h
i
j
?

FIG. 8. Evolution of *G.* (*Glyptograptus*), *G.* (*Pseudoglyptograptus*), *Rhaphidograptus* and *Cystograptus*: a, from the left, SM A20413, SM A10012 and SM A10010; respectively Pumpsaint, Torver Beck and Dobb's Linn, showing the considerable degree of variation exhibited by *G. persculptus* populations; b, LU 4043; c, HUR S75,9.4/74; d, LU 4049; e, BM(NH) Q1583; f, BM(NH) Q1594; g, SM A81977; h, LU 57544 and, below, LU 57543; i, LU 4098; j, SM A23607. All figures ×3½. ['aff. *nickoleyi*' should read 'aff. *nikolayevi*'.]

While it is not possible to be very certain of their evolutionary origins with respect to particular species, the general resemblance of *G.* (*P.*) *vas* to *G. sinuatus* is striking (Fig. 8), and the latter first appears earlier. Such a lineage would involve acquisition of a concavoconvex supragenicular wall, apertural eversion and, further, an upright ventral apertural process in some species (Fig. 8). Increasingly sigmoidal

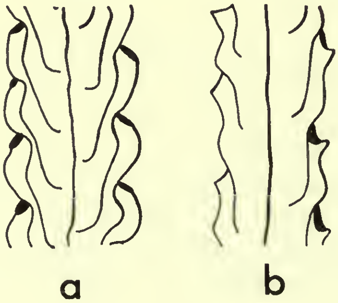


FIG. 9. Comparison of the distal thecae of *Cystograptus penna* (Nicholson), a, SM A23607, *acinaces* Zone, with *Glyptograptus* (*Pseudoglyptograptus*) *vas*, b, GSM WEG 4058, *magnus* Zone. Both figures ×10.

thecal tubes is a feature of many Silurian graptoloids (e.g. *Cystograptus*) as is thecal eversion (*Monograptus*, *Monoclimacis* etc.), but the combination of some eversion with an upright ventral apertural process, effectively a feature of *introversion*, is unusual and can only be paralleled to a slight extent by *Pribylograptus* (Fig. 17).

G. (*P.*) spp. 1 and 2 are closely similar forms from succeeding horizons and are doubtlessly related, whilst *G.* (*P.*) *rhayaderensis* is a striking aseptate form possibly related to *G.* (*P.*) *vas* (Fig. 8). We are unable to suggest any evolutionary relationships at present for *G.* (*P.*) *tabukensis*, which is known only from Saudi Arabia.

8. *Dimorphograptus* (*'Dimorphograptus'*). Dimorphograptids *sensu lato* include forms with three different thecal types; broadly, climacograptid, glyptograptid and orthograptid. The first is now embraced by the genus *Rhaphidograptus* Bulman, although it will be shown below (p. 24) that the type species *R. toernquisti* (Elles & Wood) (Pl. 1, figs 1–2; Pl. 2, fig. 1) probably evolved from a particular glyptograptid species. The detailed thecal structure of the other two dimorphograptid types is a little uncertain, but it is at least quite clear that they are not *simply* of glyptograptid or orthograptid type (Fig. 10). Bulman (1970) has pointed out that some forms show apparent apertural isolation, a typically Silurian evolutionary feature (p. 91), while others show undulating and possibly more complex thecal apertures (Fig. 10). It is also possible that strictly orthograptid thecae are absent in these groups and that they are all basically glyptograptid.

However, it is not unreasonable to suppose that *D.* (*'Dimorphograptus'*) types, with broadly glyptograptid thecae, evolved from one or more species of *Glyptograptus*, or that *D.* (*'Bulmanograptus'*), with orthograptid thecae, evolved from *Orthograptus* (but see p. 28). The type species of *Dimorphograptus* is *D. elongatus* Lapworth (Pl. 1, fig. 3), which has a long uniserial portion and glyptograptid thecae, and, like other dimorphograptids *sensu lato* (except *Rhaphidograptus*), has the initial bud upwardly directed at its origin. The distal portions of the rhabdosome (Fig. 11) are indistinguishable from *Glyptograptus*.

Bulman (e.g. 1970) has discussed the development of a uniserial from a biserial rhabdosome and this will not be further discussed here except to note that loss or reorientation of th1^2 is necessary as well as a septate rhabdosome. Since dimorphograptids are preceded in the record by *M. ceryx* Rickards & Hutt they are probably best regarded not as evolutionary intermediates between biserials and uniserials, but as biserials which have been partially affected by Silurian evolutionary trends

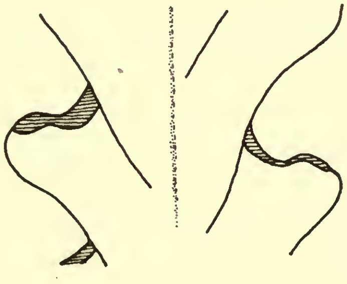


FIG. 10. Diagrammatic sketch of thecae of *Dimorphograptus* sp., GSM, from Bryn Dowsi borehole at 119·10 m, *cyphus* Zone; illustrating undulating thecal aperture. ×20.

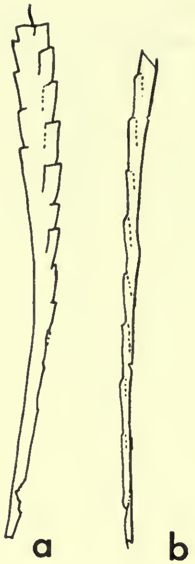


Fig. 11. *Dimorphograptus elongatus* Lapworth. a, LU 57506; b, LU 57507, School Beck, Lake District, *atavus* Zone. Both figures × 5.

including thecal isolation and growth of genicular hoods (p. 91) as well as partial production of a uniserial rhabdosome. It is noteworthy that the successful and quite rapid introduction of a new character in one graptoloid group is quite often followed by similar but apparently abortive introduction in another. In this case the environmental pressures resulting in the uniserial rhabdosomes must have waned shortly afterwards, since there is no evidence at all that uniserial graptoloids were again to develop from biserial ancestors: the waning period was effectively the time span of the *acuminatus* and *atavus* Zones during which the genera *Rhaphidograptus*, *Dimorphograptus sensu lato* and *Akidograptus* appeared. No *Dimorphograptus* species appear after the *cyphus* Zone, and very few rhaphidograptids, but there is a tendency to protraction of the proximal end of biserials even as late as the *convolutus* Zone (p. 88 below).

9. *Rhaphidograptus*. The genus as originally defined included only *Climacograptus toernquisti* Elles & Wood, but the definition has since been extended by its author (Bulman 1955, 1970) to include dimorphograptids with climacograptid thecae. Thus *D. extenuatus* Elles & Wood, the type species of *Metadimorphograptus* (Přibyl 1948), is now included. Whilst it is quite reasonable that rhaphidograptids should have evolved from *Climacograptus* by a parallel of the same tendencies affecting glyptograptids, we nevertheless note the great difficulty in distinguishing distal thecae of *R. toernquisti* from those of *G. sinuatus* and *G. persculptus*. We prefer, in fact, to derive *R. toernquisti* from a slender form of *G. persculptus* (see Fig. 8), the biserial portions of which seem quite identical to that of *R. toernquisti*.

Both *R. toernquisti* and *R. extenuatus* appear in the *atavus* Zone, the latter, with its longer uniserial portion, somewhat earlier in the Lake District than

R. toernquisti. The following species have been recorded at the same and higher levels by Obut & Sobolevskaya (1967, 1968) : *R.* ? *vicinus* Obut & Sobolevskaya ; *R. maslovi* Obut & Sobolevskaya ; *Agetograptus secundus* Obut & Sobolevskaya ; *A. primus* Obut & Sobolevskaya ; *A. zintchenkoae* Obut & Sobolevskaya. Of these *A. zintchenkoae* and *R. maslovi* have thecae which are more obviously glyptograptid, while *A. secundus* may represent the occurrence of the rhaphidograptid condition in a species of orthograptid origin. One of us (R. B. R.) has examined the originals of all these Russian species and is of the opinion that with *R. toernquisti* and *R. extenuatus* they represent a group with glyptograptid ancestors, in which greater geniculation has occurred than in the derivatives *D.* (*'Dimorphograptus'*) and *D.* (*'Bulmanograptus'*). It should be added that in any bedding plane with numbers of specimens of *A. secundus* some will have the long (rhaphidograptid) th1^2 while others will be of normal biserial type : another case of Jaanusson's (1973) dithyrial populations (p. 38).

10. *Cystograptus* Hundt (1942) was emended by Jones & Rickards (1967), who suggested that the type species had the same double sigmoid (ogee) thecal curvature as *C. penna* which was studied in three-dimensional material. Teller (1969) presumably did not accept the suggestion but one of us (J. E. H.) later obtained Lake District specimens of *C. vesiculosus* (Fig. 8i, p. 22 ; Pl. 2, fig. 7) conclusively demonstrating the ogee curvature. As far as we are aware no other cystograptids have been described, but Mu & Lee (1958) describe apparently identical thecal structures in *Glyptograptus* ? *curvithecatus* Mu & Lee from the *hirundo* Zone of west Chekiang. It is possible that some mistake in horizon or locality has been made by Mu & Lee, although the claimed associated fauna is undoubtedly Arenig.

Fig. 9 depicts a possible morphological relationship between *Cystograptus* and *G.* (*Pseudoglyptograptus*). Continued growth of the thecal tube over the geniculum of the latter genus would result in the genus *Cystograptus*. Such an *evolutionary* relationship is precluded by the early appearance of *Cystograptus* (*acuminatus* to *cyphus* Zones), but the derivation of both genera from *Glyptograptus* seems likely : a member of the *G. persculptus* plexus seems a possible contender as the ancestor of *C. vesiculosus* (Fig. 8).

The main Silurian tendencies displayed by *Cystograptus* are, therefore, the thecal elongation and apertural eversion. The pronounced nemal vanes (Jones & Rickards 1967) occur in some form in a number of Silurian biserial groups and it is possible that the number of species possessing them greatly exceeds that in the Ordovician : development of vanes is probably dominantly a Silurian tendency of which one of the first representatives is *Cystograptus.*

11. *Orthograptus.* The genus is quite well represented in the late Ordovician by various forms of *O. truncatus* Lapworth (Pl. 1, fig. 7), which species also persists rarely into the *acuminatus* Zone of the Silurian. Within the Silurian, however, orthograptids are only rarely represented by more than one or two species in any one zone, and each species usually forms only a small proportion of the graptoloids

encountered. In the Howgill Fells, for example, Rickards (1970) collected only about twenty specimens of *Orthograptus* whilst Hutt (1974) recorded only ninety specimens from a collection of some 20,000 Llandovery graptoloids. The genus is discussed here, rather than as an 'Ordovician remnant', since it may well have given rise directly to three further groups or genera (sections 12–14 below), and ultimately to all the retiolitid genera (sections 16–19 below).

Evolution within *Orthograptus* itself is difficult to discern for the same reasons that apply to *Diplograptus*, namely paucity of species and specimens. Neither Toghill (1968a, b) nor Hutt (1974) record *Orthograptus* from the *persculptus* Zone, but both identified *O. truncatus abbreviatus* Elles & Wood in the *acuminatus* Zone. Hutt in addition regards *Akidograptus acuminatus* (Nicholson) as an orthograptid with a protracted proximal region, an interpretation with which all the present writers agree (p. 28). The only record in beds possibly partly equivalent to the *atavus* Zone is *O. eberleini* Churkin & Carter from Alaska, whilst the succeeding orthograptids appear in the following order: *O. mutabilis* (*acinaces* and *cyphus* Zones), *O. cyperoides* and *O. bellulus* (*triangulatus* to *sedgwickii* Zones), *O. obuti* (*triangulatus* Zone), *O. insectiformis* (*magnus* to *convolutus* Zones).

O. eberleini is a diminutive species with a small sicula, but *O. mutabilis* has the long free sicula and proximal end typical of the succeeding *O. cyperoides* and *O. insectiformis*. Hutt (1974) has shown that, like *O. insectiformis*, *O. cyperoides* and *O. bellulus* also have thecal spines albeit somewhat more slender than in *insectiformis*, which also exhibits a strongly divided virgella in the form of a meshwork (Hutt 1974; Rickards & Koren' 1974). It is very likely that *O. mutabilis*, if not *O. eberleini*, gave rise to *O. cyperoides*, *O. bellulus* and then to *O. obuti* and *O. insectiformis* by development of increasingly long and robust thecal spines. The last species to appear, *O. insectiformis*, develops a virgella meshwork, as does *O. obuti* Rickards & Koren' (*triangulatus* Zone of the southern Urals). Fig. 12 depicts the suggested simple progression which, whilst fitting the known record and morphology quite well, perhaps hides the fact that the species are not well known from three-dimensional material.

Another problem which we have no wish to avoid is the actual origin of Silurian orthograptids. It is conceivable, though unlikely, that *O. truncatus abbreviatus* gave rise to *O. eberleini* and hence to the lineages of Fig. 12. But there are no indications in either species of the *mutabilis* proximal end and they are best regarded as the last representatives of '*Rectograptus*' (Přibyl 1947). Thus it is possible that the remaining Silurian orthograptids have their origins in a Silurian genus such as *Glyptograptus*. *Glyptograptus* ? *enodis* and *G.* aff. *nikolayevi* (Fig. 8), from the *cyphus* and *acinaces* Zones respectively, have proximal ends much closer to the *O. mutabilis* type. Furthermore, it is known that later glyptograptids develop thecal spines.

Finally, it is of interest that these observations on *Orthograptus* do not lend much support to Přibyl's classification of orthograptids into those with apertural spines (*Orthograptus quadrimucronatus*) and those without (*Rectograptus truncatus*): Silurian forms have previously been placed in *Rectograptus* by those workers favouring such generic distinctions.

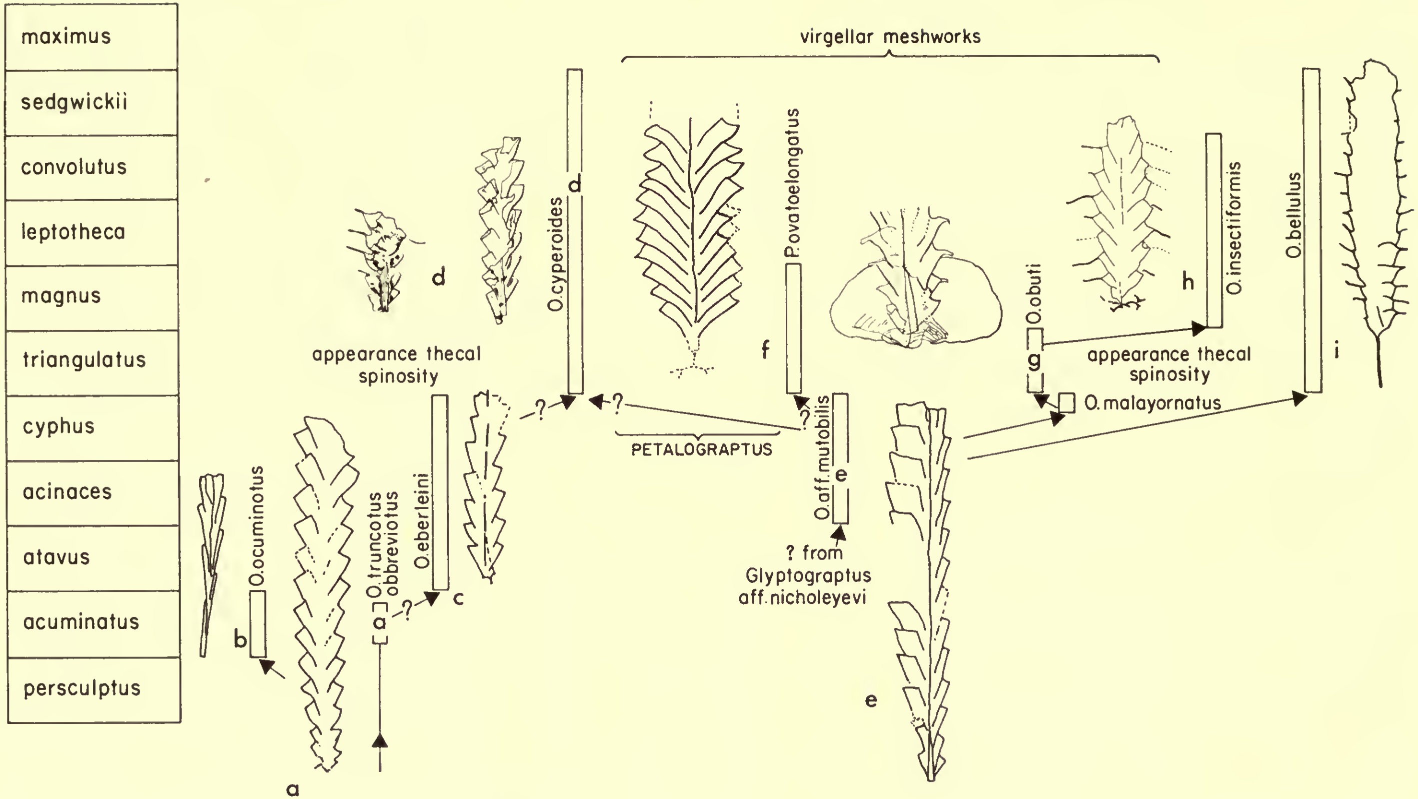

maximus
sedgwickii
convolutus
leptotheca
magnus
triangulatus
cyphus
acinaces
atavus
acuminatus
persculptus
virgellar meshworks
appearance thecal spinosity
appearance thecal spinosity
PETALOGRAPTUS
O.acuminatus
O.truncatus obbreviatus
O.eberleini
O.cyperoides
P.ovatoelongatus
O.aff.mutabilis
? from Glyptograptus aff.nicholeyevi
O.obuti
O.malayornatus
O.insectiformis
O.bellulus
a
b
c
d
e
f
g
h
i
?

Fig. 12. Evolution of *Orthograptus*: a, BM(NH) Q2866, *anceps* Zone; b, HUR S/1; c, USNM 161783; d, from the left, LU 4085 and LU 4081; e, LU 4074; f, LU 57537; g, after Rickards & Koren' (1974); h, BM(NH) Q3112; i, LU 4090. All figures × 4½. ['aff. *nicholeyevi*' should read 'aff. *nikolayevi*']

12. *Orthograptus acuminatus.* This species (Pl. 2, fig. 3) is usually grouped in *Akidograptus* with *A. ascensus*, the type species of the genus which has climacograptid thecae. *O. acuminatus* has broadly orthograptid thecae but shares with *A. ascensus* a protracted proximal end and an elongated sicula except in the subspecies *O. acuminatus praematurus* Davies. This last looks like a normal orthograptid with a pointed proximal end and a slight thecal geniculation. Thus *O. acuminatus* is best regarded as an orthograptid which has assumed the typically Silurian features of elongated thecae and sicula and protraction of the proximal end. There is no uniserial portion in either *A. ascensus* or *O. acuminatus* and each resulted from similar environmental pressures exerted upon representatives of *Climacograptus* and *Orthograptus* respectively. Other species similar to *O. acuminatus* have been described : *A. zhejiangensis* Yang (1964), *A. giganteus* Yang (1964), *A. a. precedens* Münch (1952), *A. priscus* Hsü (1934) ; it may become desirable eventually to erect a new genus to embrace this rather unusual and stratigraphically restricted group of orthograptids, particularly in view of the fact that the thecae, although broadly orthograptid, have a slight geniculum and rather undulating, fractionally introverted thecal apertures. *A. giganteus* has climacograptid-like proximal thecae and orthograptid-like distal thecae, and may represent the imposition of the Silurian *Diplograptus* trend upon a climacograptid or glyptograptid stock (p. 16).

13. *Dimorphograptus* ('*Bulmanograptus*'). Some reference has been made above (p. 23) to these forms typified by *D. confertus* Nicholson. The thecae are certainly not of simple orthograptid type and it is far from certain that they are of orthograptid origin. Indeed we feel that much further investigation of this group of dimorphograptids is required before any firm suggestions about origins can be made. In the meantime it is noted that some species display apparently isolated thecal apertures (*D. decussatus*), a typically Silurian feature, whilst others have possibly complex thecal apertures (Fig. 10).

14. *Petalograptus.* Petalograptids range from the *triangulatus* to the *crenulata* Zone but are particularly abundant and more varied at the lower end of the range (Fig. 1). Many of the described petalograptids (e.g. *P. palmeus* (Barrande), *P. elongatus* Bouček & Přibyl ; Figs 13a, b) bear close resemblance to *Orthograptus* species and it is without doubt that their origins lie within this genus : indeed these *Orthograptus* derivatives clearly fitted the new Silurian environment better than the *Orthograptus* species themselves which, as we show above (p. 26), are somewhat restricted in numbers of species and specimens.

Petalograptus species retain a small sicula but the proximal end nevertheless displays pronounced protraction which is achieved by strong upward growth of all the thecae except the initial bud of th1^1. The great length of the thecal tubes, coupled with this upward growth, results in a foliate, tabular rhabdosome. In addition, the genus may be distinguished from *Orthograptus* by the more common nemal vanes and the gentle ventral concavity (in profile) of the thecae.

At the specific level some of the forms described by Bouček & Přibyl (1941) provide morphological intermediates : *P. elongatus* must be considered a borderline

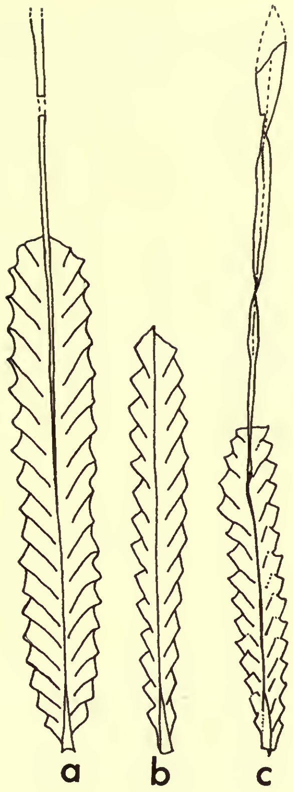


FIG. 13. Diagram indicating range of variation in *Petalograptus*. a, *Petalograptus palmeus palmeus* (Barrande) after Bouček & Přibyl (1941) ; b, *P. elongatus* Bouček & Přibyl (1941) ; c, *Petalograptus* sp. SM A75383, *crispus* Zone, Lake District ; each has distinct orthograptid features and b is best regarded as a borderline petalograptid. All figures × 5.

petalograptid. Nevertheless, some of the earliest forms such as *P. ovatoelongatus* are the most typical of petalograptids. One problem of the origin of such *triangulatus* Zone species as *P. ovatoelongatus* and *P. minor* (Pl. 2, fig. 2) is that the number of known, possible, *Orthograptus* ancestors is very limited (p. 26). *O. mutabilis* from the *acinaces* and *cyphus* Zones has a similar rhabdosomal and thecal appearance and a sicula some 2 mm in length, and must be regarded as the most likely ancestor of *P. ovatoelongatus*, which, unlike some later petalograptids, has a sicula 2 mm long at least in the Howgill Fells (Rickards 1970).

Subsequent evolution within *Petalograptus* is difficult to understand. Preliminary work by two of us (R. B. R. & J. E. H.) suggests that infraspecific variation may be rather greater than in species of contemporary genera. It is also possible that the genus is polyphyletic and that some of the slim petalograptids of higher horizons (e.g. *P. wilsoni* Hutt) may derive from some of the last orthograptids although the known species are spinose (Fig. 12). Certainly there seem to be two groups persisting throughout the range of petalograptids, the one a robust group basically resembling *O. ovatoelongatus*, the other with more slender species (Pl. 3, fig. 2) resembling *P. wilsoni*. Specific lineages within the *Petalograptus* species pose an interesting problem for future research.

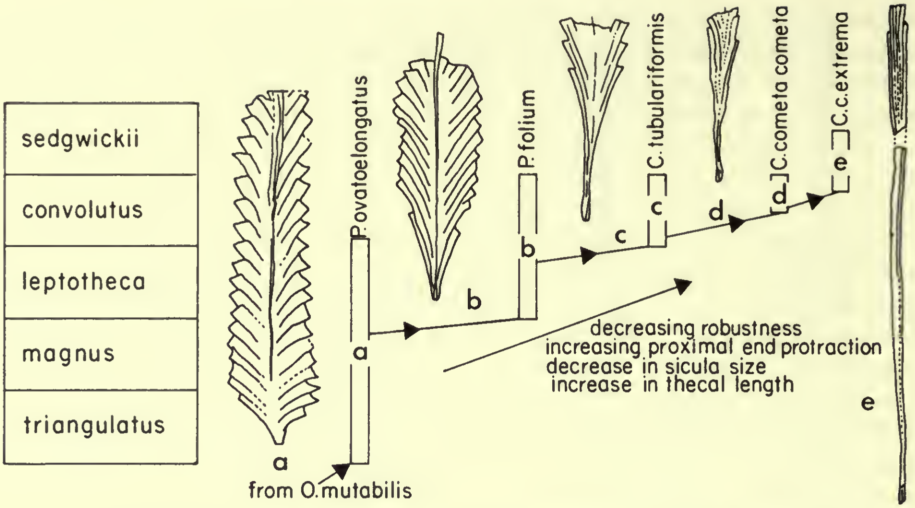

sedgwickii
convolutus
leptotheca
magnus
triangulatus
a
from O. mutabilis
P. ovatoelongatus
a
b
P. folium
b
c
C. tubulariformis
c
d
C. cometa cometa
d
e
C. c. extrema
decreasing robustness
increasing proximal end protraction
decrease in sicula size
increase in thecal length
e

FIG. 14. Derivation *Cephalograptus* from *Petalograptus*: a, GSM CV8930; b, after Bouček & Přibyl (1941); c, BM(NH) Q102; d, LU 57546; e, LU 57551. All figures ×2½.

15. *Cephalograptus* Hopkinson (1869) is an extreme development of *Petalograptus*, embracing few species, in which protraction of the proximal end (Fig. 14) has been carried out to such an extent that the early thecae (1^1, 1^2) are probably the longest known graptoloid thecae. Specimens from the Lake District are known with thecae over 17 mm long whilst Elles & Wood (1908) record specimens with thecae of 30 mm length.

There is probably a stratigraphical and evolutionary succession from a form such as *P. ovatoelongatus* (*triangulatus* to *convolutus* Zone), to *P. folium* (*leptotheca* and *convolutus* Zones), to *Cephalograptus cometa* (top of *convolutus* to *sedgwickii* Zone). With the exception of *Dimorphograptus elongatus* (*atavus* Zone), which resembles an attempted monograptid, *C. cometa* may be regarded as the most extreme example of proximal end protraction, exceeding even *A. ascensus* and *R. toernquisti*. Only *C. cometa cometa* (Geinitz), *C. c. extrema* Bouček & Přibyl and *C. tubulariformis* Nicholson have been described: the species *O. acuminatus* Nicholson was placed doubtfully in *Cephalograptus* by Elles & Wood (1908) but it should be accommodated neither there nor in *Akidograptus* (p. 28); it is best considered an orthograptid with a protracted proximal region.

B. The Retiolitids

The most spectacular gap in the record between apparently similar groups in the Ordovician and Silurian is that between the (Ordovician) Archiretiolitinae and the Silurian retiolitids *sensu lato* – which do not appear until the *argenteus* Zone. As far as we are aware no retiolitids have yet been obtained from the *anceps* to the *magnus* Zones inclusive, which indicates a Silurian ancestry amongst the biserial graptolites for the Silurian retiolitids. Silurian retiolitids fall broadly into two subfamilies, the Retiolitinae (? *triangulatus*, ? *magnus*, *argenteus* to *centrifugus* Zones, ? *murchisoni* Zone) and the Plectograptinae (Middle Wenlock, top *riccartonensis* Zone, to post *leintwardinensis* Zone strata). These groups are discussed below in sections 16–19).

16. *Retiolites*, *Stomatograptus* and *Sinostomatograptus*. The genus *Pseudoretiolites* Bouček & Münch (1944) was included in *Retiolites* by Bulman (1970) and Hutt (1974), but here we prefer to treat it separately (section 17, p. 33) since, as defined, it spans the *argenteus* to *maximus* Zones at the most whereas *Retiolites* (restricted) first appears in the *griestoniensis* Zone (? *crispus* Zone).

Retiolites geinitzianus shows considerable variation in rhabdosomal form and is clearly in need of considerable revision. Forms not unlike *R. g. angustidens* Elles & Wood, a typical *centrifugus* Zone form in Britain, occur as low as the *griestoniensis* Zone in the Howgill Fells, North America and the U.S.S.R., whilst robust forms occur less commonly at the same level. The long broad forms (i.e. typical *R. geinitzianus*) bear a striking resemblance to *Petalograptus altissimus*, to such a degree in fact that they are often mistaken for each other in museum collections. The derivation of *R. geinitzianus* from *P. altissimus* would involve, however, considerable periderm reduction, the development of a clathria, and, a more difficult morphological step perhaps, the incorporation of the nema or virgula in one of the rhabdosomal lateral walls. This last step is not always taken in Silurian retiolitids (p. 36).

The recent work on the periderm ultrastructure of retiolitids (Urbanek & Rickards 1974) does not preclude such a derivation, but the clathrial ultrastructure is, as might be expected, rather specialized and extremely electron dense. Some recent work on retiolitids (Skoglund, personal communication, and 2nd Soviet Graptolite Conference in Tallin) has shown that the clathria and reticula may be underlain by a thin but complete periderm, *possibly* of fusellar tissue.

Stomatograptus and *Sinostomatograptus*, the latter recently recorded outside China for the first time (Hutt 1974; Fig. 15), are basically similar to *Retiolites* and the thecae are essentially orthograptid or petalograptid. Since orthograptids are unknown in the highest Llandovery (Fig. 12) petalograptids would seem to be the only likely ancestors to all three genera *Retiolites*, *Stomatograptus* and *Sinostomatograptus*. The supposed lacinia in the last of these requires further study, but there would seem to be no grounds at present for linking the genus with *Pseudoplegmatograptus* (Fig. 15; p. 33) rather than with *Retiolites* and *Petalograptus*. *Stomatograptus*, like the much earlier *Pseudoretiolites*, has a solid interthecal septum but clearly in this feature cannot be regarded as very much different from those forms of *R. geinitzianus* which have a thin but continuous layer of periderm beneath the clathria and reticula. Both *Stomatograptus* and *Sinostomatograptus* have a median row of large pores, or stomata, along the lateral walls. These do not coincide with the thecae themselves and are almost certainly a strengthening feature of the reticula: those retiolitids lacking a strengthening of the lateral walls often tear

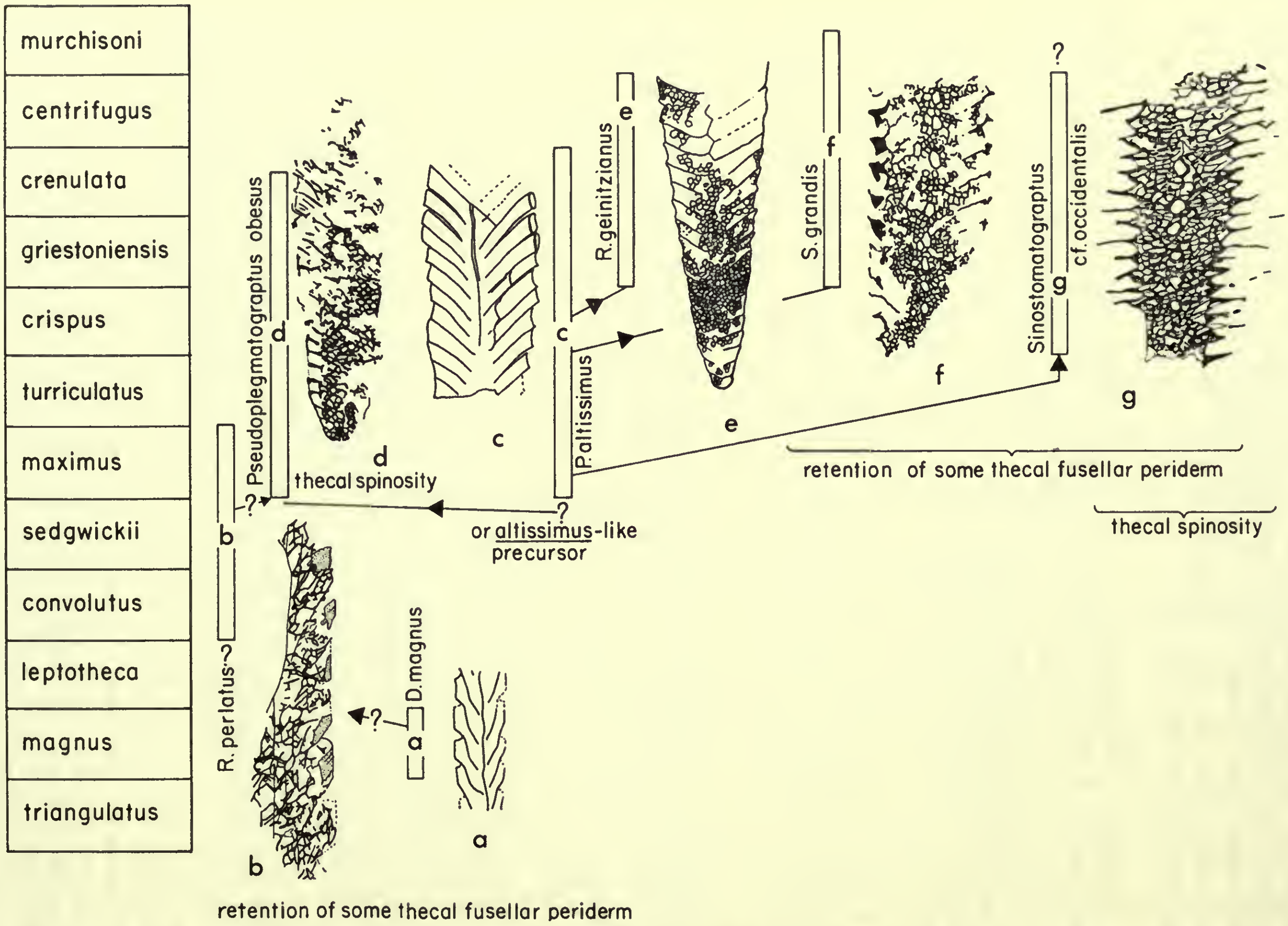

murchisoni
centrifugus
crenulata
griestoniensis
crispus
turriculatus
maximus
sedgwickii
convolutus
leptotheca
magnus
triangulatus
R. perlatus-?
b
?
Pseudoplegmatograptus obesus
d
thecal spinosity
d
c
c
P. altissimus
?
or altissimus-like
precursor
R. geinitzianus
e
e
S. grandis
f
f
Sinostomatograptus
g
cf. occidentalis
?
g
retention of some thecal fusellar periderm
thecal spinosity
D. magnus
a
?
a
b
retention of some thecal fusellar periderm

FIG. 15. Evolution of Llandovery retiolitids: a, LU 4047; b, LU 57500; c, SM A21608; d, LU 57503; e, HUR 25W/6; f, BM(NH) Q3132; g, SM A83975. All figures ×5.

along the length of them. *Plectograptus* ? *bouceki* Rickards (section 18 below, Fig. 16) is often found torn along its length.

There are very few species of the stomata-bearing genera, but a whole variable plexus of forms referable to *R. geinitzianus sensu lato* : the nature of this plexus needs unravelling before further specific lineages can be proposed.

17. *Pseudoretiolites* and *Pseudoplegmatograptus*. Of these two genera *Pseudoretiolites* occurs much earlier, possibly as early as the *triangulatus* Zone (Elles & Wood 1918). As well as having a solid links interthecal septum we now know from isolated Swedish specimens in the collection of two of us (R. B. R. & J. E. H.) that this is composed of fusellar tissue and displays clear growth lines (Fig. 15). Further, there is an apparent genicular homologue and an almost vertical supragenicular wall : the clathria is poorly developed, the reticula fibrous, and the nema possibly central.

The nature of the thecae suggests an origin not from *Orthograptus* or *Petalograptus* but from *Climacograptus* or *Diplograptus*. The short supragenicular wall and long excavations, as well as the dorsoventral width (up to 5 mm) and shape and size of the rhabdosome, recall *D. magnus* H. Lapworth (cf. Figs 15a, b) which may precede *P. perlatus*, although there is certainly some doubt about the first occurrence of the latter. In any event a *Diplograptus* ancestor seems a distinct possibility for *Pseudoretiolites*. The writers are aware of the following species in *Pseudoretiolites* : *P. perlatus* (Nicholson) ; *P. petalograptoides* Bouček & Münch ; *P. thuringicus* Bouček & Münch ; *P.* sp. Bouček & Münch (1952) ; *P. dentatus* Bouček & Münch (1944). One of these, *P. petalograptoides*, closely resembles *Petalograptus ovatus*, possibly suggesting an origin in this genus and at the same time indicating that *Pseudoretiolites* may be polyphyletic.

Pseudoplegmatograptus probably appears in the *sedwickii* Zone and ranges into the *crenulata* Zone. It thus overlaps with *Sinostomatograptus* which also possesses a lacinia and indistinct clathria. However, the presence of a sclerotized interthecal septum in *Sinostomatograptus* probably indicates a more recent origin from *Petalograptus*, rather than from *Pseudoplegmatograptus* which apparently lacks thecal fusellar periderm.

Because of the apparently ill-defined clathria the thecae of *Pseudoplegmatograptus* are difficult to discern, but they may be essentially of orthograptid type (Bulman 1970 : fig. 95.7) with thecal spines and a supported and somewhat nebulous lacinial network. Because of the dorsoventral width up to 6 mm in most pseudoplegmatograptids such thecae must be very long and inclined to the axis of the rhabdosome at quite a high angle, at least adaperturally (Fig. 15d), perhaps suggesting a link with the petalograptids or orthograptids. Derivation from *Pseudoretiolites* seems unlikely if the structure of the latter is as illustrated in Fig. 15b. We would like to emphasize here, however, that there are probably other retiolitids to be discovered at these levels, particularly by chemical techniques (e.g. Hutt, Rickards & Skevington 1970) : retiolitid structures in the rock are exceedingly difficult to distinguish. Until the structure is worked out in the same detail as in other retiolitids the origin of *Pseudoplegmatograptus* must remain a matter for speculation, but it seems highly unlikely that it could give rise to any of the later retiolitid genera (see Fig. 15).

18. *Plectograptus* ?, *Plectograptus* and *Paraplectograptus*. Following the last occurrences of *Retiolites* and *Stomatograptus* in the low Wenlock (probably in the *centrifugus* or *murchisoni* Zones ; Fig. 16) there is a gap, at least equivalent to most of the *riccartonensis* Zone, where no retiolitids have been recorded. One of us (R. B. R.) has examined specimens from Podolia, possibly referable to *Plectograptus* ?, provided by Dr Koren', which occur with a *murchisoni* Zone assemblage including *C. m. murchisoni*. This suggests that there are yet other retiolitids to be discovered in the low Wenlock strata. Otherwise the earliest form to *appear* in the Wenlock is *P.* ? *textor* Bouček, a species similar to the succeeding *Plectograptus* ? *bouceki* Rickards. The former was considered by Rickards (1967) to have orthograptid-like thecae throughout and the latter to have proximal 'climacograptid' thecae and distal 'orthograptid' thecae. Such a species as *P.* ? *bouceki* could, therefore, provide a link between the low Wenlock *Retiolites* (with 'orthograptid' thecae) and the upper Wenlock *Plectograptus* species (with 'climacograptid' thecae). There are no other possible ancestors from which *P.* ? *bouceki* could be derived, for biserials with a solid periderm became extinct with *P. altissimus* (but see p. 17), and the only biserials to survive into the low Wenlock are referable to *Retiolites* or *Stomatograptus*. These latter may, therefore, have given rise to the Podolian species, or to *P.* ? *bouceki*, and the whole relatively successful development of late Wenlock, low Ludlow retiolitids hinges upon this group.

Plectograptus (Fig. 16c) has a central nema and in this respect contrasts with *Retiolites*. Since *Retiolites* must have acquired its laterally positioned nema from an ancestor with a central nema (p. 31) the reversion to the earlier condition seems odd and is a feature not usually encountered in the evolution of the graptoloids. In *Plectograptus* ? the position of the nema is uncertain. However, as will be shown below, the position of the nema with respect to the lateral rhabdosomal wall is rather variable in the late Wenlock and low Ludlow retiolitids. On present evidence one cannot select a postulated lineage which does not require the nema to change its position at least twice.

Paraplectograptus Přibyl, from the *lundgreni* Zone, has the appearance of a much simpler *Plectograptus* (Fig. 16f) but with the nema embedded in a lateral rhabdosomal wall. The only immediate ancestors of *Paraplectograptus* are species of *Plectograptus* and *Plectograptus* ? which have a central nema. The derivation of *Paraplectograptus* from *Plectograptus* involves loss of the parietal lists, one of the ? subapertural loops, and the list connecting the ? subapertural and ? genicular lists (Fig. 16f).

19. *Gothograptus*, *Holoretiolites* and *Spinograptus*. *Gothograptus nassa* Holm appears in the top of the *lundgreni* Zone, and like *Plectograptus* has a 'climacograptid' appearance with a geniculum (armed with a genicular hood) and a supragenicular wall, defined by clathrial and reticular elements, which slopes slightly inwards towards the next aperture. The nema is at first central, as in *Plectograptus*, but

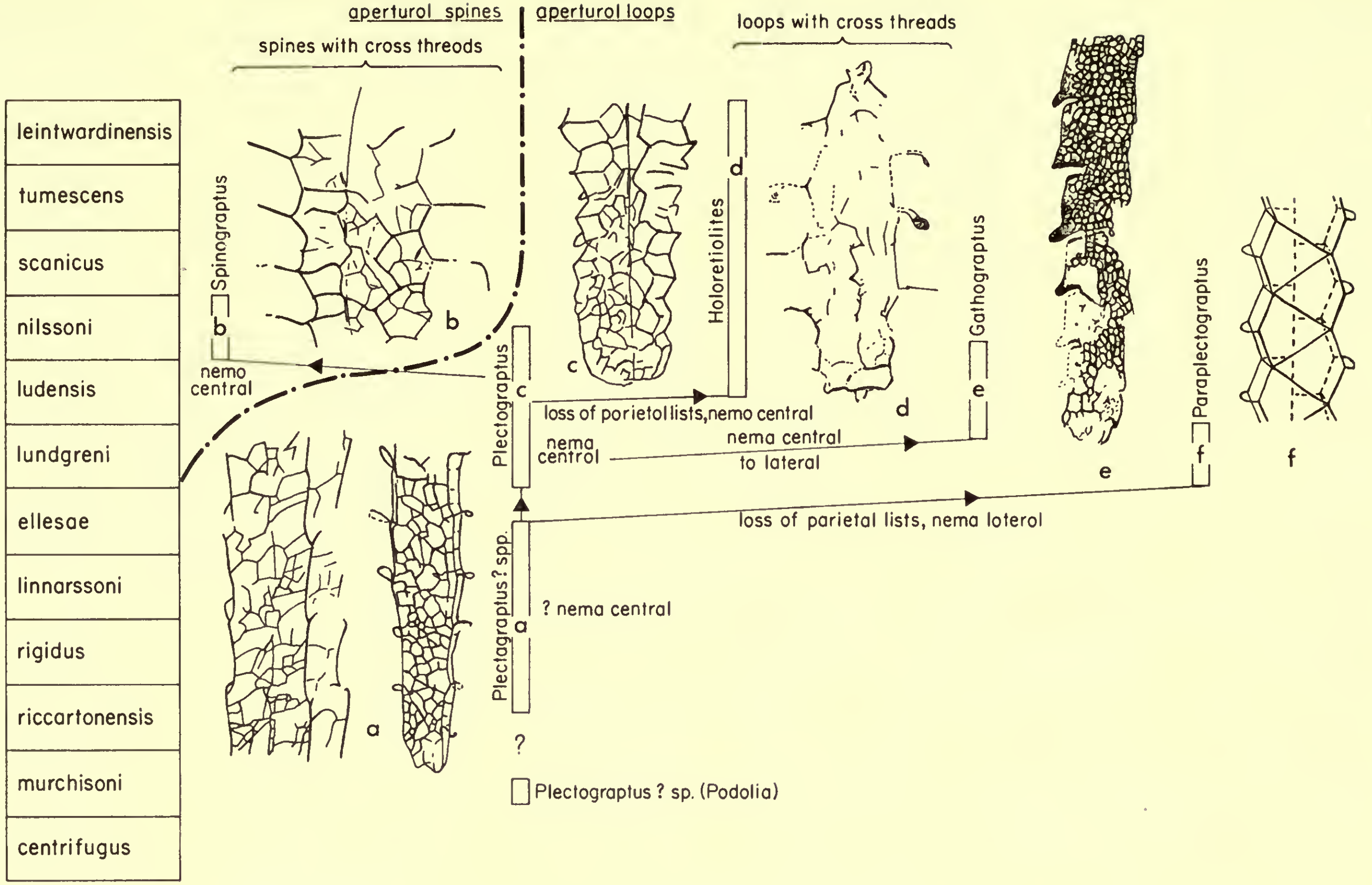

apertural spines
apertural loops
spines with cross threads
loops with cross threads
leintwardinensis
tumescens
scanicus
nilssoni
ludensis
lundgreni
ellesae
linnarssoni
rigidus
riccartonensis
murchisoni
centrifugus
Spinograptus
b
nema central
a
b
c
Plectograptus
c
Holoretiolites
d
d
loss of parietal lists, nema central
nema central
nema central to lateral
Gathograptus
e
e
Paraplectograptus
f
f
loss of parietal lists, nema lateral
Plectograptus ? spp.
a
? nema central
?
Plectograptus ? sp. (Podolia)

FIG. 16. Evolution of Wenlock and Ludlow retiolitids : a, SM A52624 and SM A52623 ; b, SM A22495 ; c, after Bouček & Münch (1952) ; d, TCD 8473 ; e, TCD 8653 ; f, after Bouček & Münch (1952). All figures ×9.

then becomes incorporated in a lateral rhabdosomal wall, finally projecting distally from the appendix. The statement by Kirk (1973), that the microfusellar hoods can hardly be genicular since the thecal tube immediately prior to the appendix has one, seems irrelevant : all preceding thecae have a geniculum and a genicular hood, but this carries no implication as to which zooid was responsible for the secretion of them. In fact, the zooid beneath the hood was almost certainly the builder in each case.

It seems likely that *Paraplectograptus* was too specialized to give rise to *Gothograptus*, leaving *Plectograptus* as the only possible source. Any lineage from *Plectograptus* to *Gothograptus* involves the development of a denser reticulum late in the growth of the colony, and the change from a regular subhexagonal clathria to an irregular one with only a suggestion of the zigzag list in some specimens. As in the evolution of *Paraplectograptus*, the parietal lists are probably lost entirely.

Holoretiolites has a short nema, central in position, and differs from *Gothograptus* in tapering more rapidly distally and in lacking a reticulum. The thecae are still of climacograptid type, and it may be mentioned that whatever evolutionary lineages are detected in the future, the high Wenlock association of retiolitids with climacograptid thecae (*Plectograptus*, *Gothograptus* and *Holoretiolites*) has evolved through *Plectograptus* ? from species of *Retiolites* with more or less orthograptid thecae. *Holoretiolites* may well have evolved from either *Gothograptus* or *Plectograptus*, but the latter is more probable since *Holoretiolites* still has a pronounced zigzag list.

Spinograptus, like all these groups, is represented by very few species. The zigzag list is still retained, as are the parietal lists, but the apertures have paired spines (Fig. 16b) directed horizontally and ventrally. The known species have all the appearance of a *Plectograptus* with apertural spines and a fine reticulum, and it is from this genus that the writers feel *Spinograptus* evolved. The nema remains central in position.

In all the above suggestions for evolution within the retiolitids the clathrial elements seem to be the most important in defining the thecal type and in defining changes during evolution. The reticulum appears to be randomly distributed between the genera and species, and presumably represents vacillating attempts at a confining periderm. An interpretation of the nema's position is very difficult, but presumably the sicula in retiolitids is to one side of the rhabdosome, as in *Petalograptus*, and in consequence the nema could be easily incorporated in that lateral rhabdosomal wall, or just as easily left free, as for example in *Archiretiolites*.

V. MONOGRAPTINID EVOLUTION

20. The Origin of Monograptids. When Hutt & Rickards (1970) described the evolution of the earliest Llandovery monograptids no monograptid species were known below the *atavus* Zone, where three groups (*atavus*, *cyphus* and *incommodus*) appeared more or less simultaneously. Thus Hutt, Rickards & Berry (1972, abstract only) suggested a possibly diphyletic origin for the monograptids :

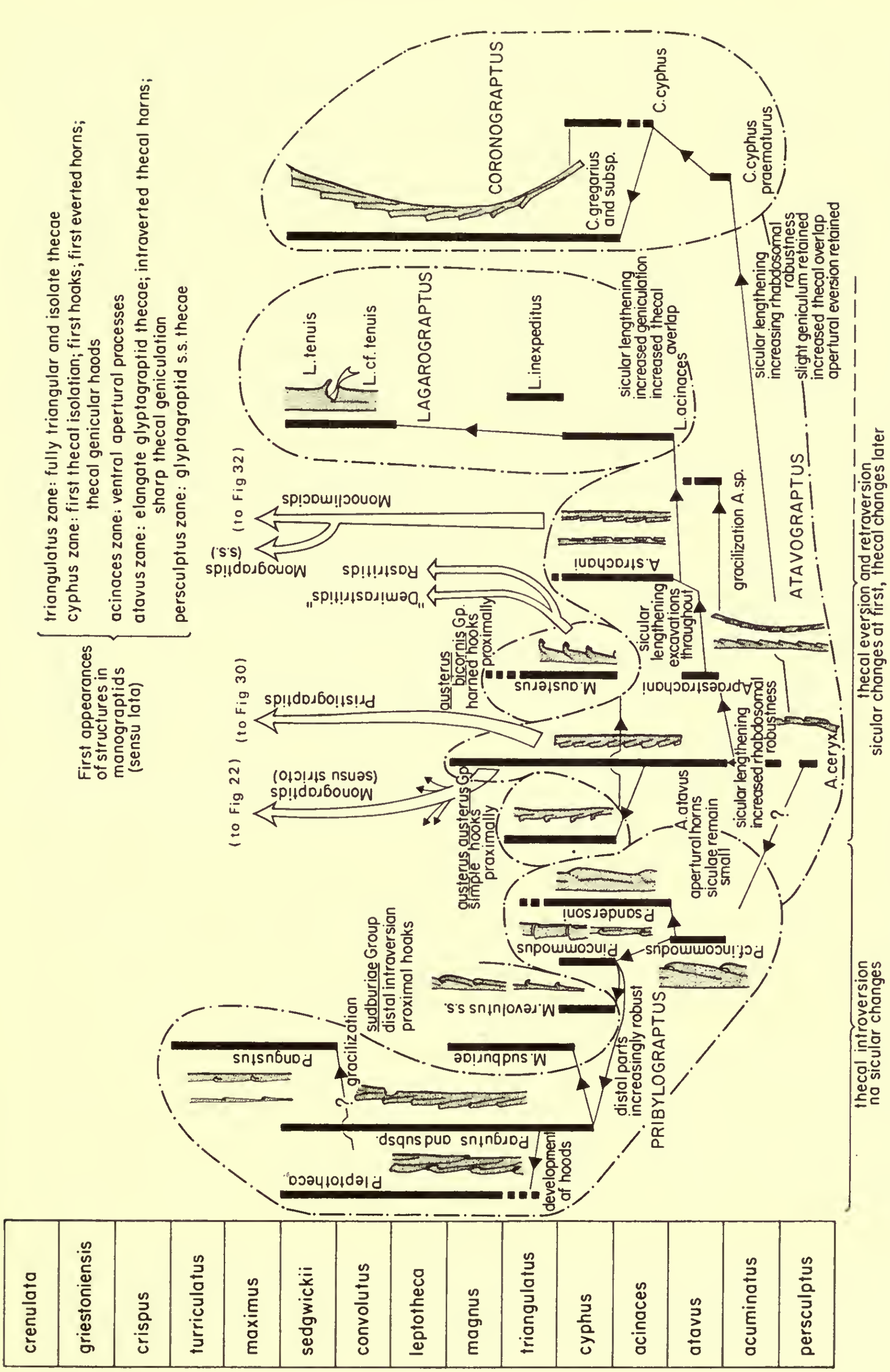

crenulata
griestoniensis
crispus
turriculatus
maximus
sedgwickii
convolutus
leptotheca
magnus
triangulatus
cyphus
acinaces
atavus
acuminatus
persculptus
First appearances of structures in monograptids (sensu lato)
triangulatus zone: fully triangular and isolate thecae
cyphus zone: first thecal isolation; first hooks; first everted horns; thecal genicular hoods
acinaces zone: ventral apertural processes
atavus zone: elongate glyptagraptid thecae; intraverted thecal horns; sharp thecal geniculation
persculptus zone: glyptagraptid s.s. thecae
(to Fig 22)
Monograptids (sensu stricto)
(to Fig 30)
Pristiograptids
(to Fig 32)
Monograptids (s.s.)
Monoclimacids
Rastritids
"Demirastritids"
P. leptotheca
P. argutus and subsp.
development of hoods
P. angustus
gracilization
M. sudburiae
sudburiae Group distal intraversian proximal hooks
M. revolutus s.s.
distal parts increasingly robust
PRIBYLOGRAPTUS
P. incommodus
P. cf. incommodus
P. sandersoni
austerus austerus Gp. simple hooks proximally
austerus bicornis Gp. horned hooks proximally
M. austerus
A. atavus
apertural horns siculae remain small
sicular lengthening increased rhabdosomal robustness
A. ceryx
A. praestrachani
sicular lengthening excavations throughout
A. strachani
gracilization A. sp.
ATAVOGRAPTUS
L. acinaces
sicular lengthening increased geniculation increased thecal overlap
L. inexpeditus
L. tenuis
L. cf. tenuis
LAGAROGRAPTUS
sicular lengthening increasing rhabdosomal robustness
slight geniculum retained increased thecal overlap apertural eversion retained
C. cyphus praematurus
C. cyphus
C. gregarius and subsp.
CORONOGRAPTUS
thecal introversion no sicular changes
thecal eversion and retraversion sicular changes at first, thecal changes later

FIG. 17. Evolution of the early monograptids including *Coronograptus*, *Lagarograptus* and *Pribylograptus*. Figures idealized, approximately × 4, except *L. tenuis* and *C. cyphus*, × 8. *C. cyphus* is drawn for convenience next to the *C. gregarius* and subsp. range rectangle.

the one line involving those species with strongly introverted thecae (the *incommodus* group, or *Pribylograptus* herein ; p. 40) and a second with essentially glyptograptid thecae (*atavus* group, *Atavograptus* herein ; p. 39 ; Pl. 4, fig. 4 ; Pl. 6, fig. 1). Between the Hutt *et al.* (1972) abstract and the actual paper, Rickards (*in* Rickards & Hutt 1970) discovered a species of *Monograptus* in the *persculptus* Zone of the English Lake District. Hutt has now recorded the same species, *M. ceryx,* in the *acuminatus* Zone on the same section. *Monograptus ceryx* is clearly referable to the *atavus* group, is known in detail from pyritized specimens (Fig. 17) and has undoubted glyptograptid thecae. This last character is so pronounced that if one places a picture of the stipe back to back with its mirror-image, the exact appearance of the biserial *Glyptograptus* is produced (Fig. 18b). It may be emphasized that if this is done with subsequent monograptids the result resembles two monograptids placed back to back, since considerable elongation of the thecal tube has already taken place. Thus the thecal spacing of *Atavograptus ceryx* is 13–15 in 10 mm and that of *A. atavus* may be as low as 5 in 10 mm. It has been pointed out by Dr Valdar Jaanusson (1973) that dithyrial populations might be expected, and we therefore suggest that the form *Glyptograptus* sp. figured by Rickards & Hutt (1970 : fig. 2d) might actually be conspecific with *A. ceryx.* The origin of the monograptid uniserial stipe from a biserial ancestor is necessarily a spectacular occurrence : one population was composed of all biserial members, whereas that succeeding may have included some uniserial forms, and the latter population may be considered to exhibit genetic polymorphy. Subsequently the uniserial rhabdosomes would predominate as their ecological advantage was conferred. The nature of this advantage is unknown, but the success of the uniserial rhabdosome from the *atavus* Zone upwards is beyond dispute.

Subsequent to the loss of genetic polymorphy, further changes, in particular the growth of a long, relatively slender, and rather variably flexuous rhabdosome,

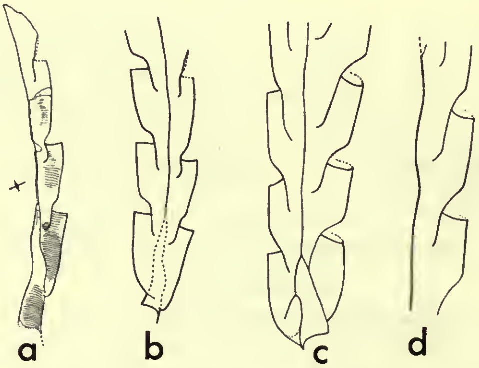


Fig. 18. a, *Atavograptus ceryx* (Rickards & Hutt), SM A67093 (arrows indicate direction of some tectonic compression of the specimen, at right angles to lineation) ; b, hypothetical biserial constructed by 'doubling up' SM A67093 and by shortening the sicula below the initial bud ; c, *Glyptograptus persculptus* s.l., SM A10012 ; d, half of A10012, idealized, to show basic similarity of thecae to those of *A. ceryx*. × 5.

took place at great speed: presumably the uniserial colonies would have had the same energy for growth as their short, stiff, immediate ancestors, and the expected changes would be increased length and, initially at least, lack of stiffness.

The occurrence of an *atavus* group species, *A. ceryx*, in the *persculptus* and *acuminatus* Zones means that once again the possible monophyletic origin of monograptids needs to be considered.

A. ceryx could certainly have given rise directly to *A. atavus* by increased length of thecae and sicula. But it is also possible that a second lineage could involve introversion of the thecal apertures, other features remaining much the same. This was suggested by Hutt *et al.* (1972 : 171), and N. Sennikov of the Institute of Geology and Geophysics at Novosibirsk informs us that he has obtained a monograptid from the *acuminatus* Zone of the Altai Mountains in which the first three thecae of the rhabdosome are of *ceryx* type but with introverted apertures, and the succeeding thecae of *ceryx* type *sensu stricto*. Such a form may be intermediate between *A. ceryx* and *P. incommodus*, and the lineage involves the proximal introduction of a new feature, namely thecal introversion (Fig. 17). Other aspects of this lineage are discussed below (p. 40).

21. The *atavus* group (*Atavograptus*) and *A. strachani*. The suggested evolution of *Atavograptus* is depicted in Fig. 17, where the range in time, and morphology of the known species, is outlined. The earliest known species, *A. ceryx*, is very reminiscent of *Glyptograptus* in appearance of thecae and thecal spacing, whilst it is possible that the initial bud of th1 grows fractionally downwards before turning distally (Rickards & Hutt 1970 : 118): such a development might be expected if the early populations derived from *Glyptograptus* were dithyrial in nature with both uniserial and biserial members (cf. Rickards & Hutt 1970 : 116, figs 2a, d).

A. ceryx occurs in the *persculptus* and *acuminatus* Zones and a Russian species possibly intermediate between *A. ceryx* and *P. incommodus* has been found in the *acuminatus* Zone in the Altai Mountains, see above. In the overlying *atavus* Zone the following species of *Atavograptus* have been recorded: *A. atavus*, *Atavograptus* sp. [= *Monograptus* sp. 2 of Hutt & Rickards 1970 : 76] (Pl. 4, fig. 5) and *A. praestrachani* sp. nov. [= *Monograptus* sp. 1 of Hutt & Rickards 1970, see p. 102]. These appear at or near the base of the *atavus* Zone.

The suggested lineage from *A. ceryx* to *A. atavus* involves an increase in length of the thecal tubes, including the sicula, and an increase in the length of the rhabdosome. Otherwise the thecae are very alike and the rhabdosomes of generally similar appearance. Other species of less certain stratigraphic and generic position include *M. renaudi* Phillipot. The Russian species, because of the thecal introversion, we suggest should be placed in *Pribylograptus* (Fig. 17; p. 40): the decision is an arbitrary one.

A. gracilis and *A. praestrachani* are morphological intermediates between *A. atavus* and *A. strachani* (Hutt & Rickards) which appears in the succeeding *acinaces* Zone. *A. praestrachani* is almost exactly intermediate, having proximal *strachani* thecae and distal *atavus* thecae (Fig. 17), and certainly gave rise to *A. strachani* by proximal introduction and spread of geniculate thecae. The lineage also involves an increase in the length of the sicula from 2·5 mm in *A. atavus* to 3·0 mm in *A. praestrachani*, and then to over 3·0 mm in *A. strachani*.

A. strachani, lacking *atavus* thecae, is included arbitrarily in *Atavograptus* since it is considered slightly closer morphologically to *A. atavus* and *A. praestrachani* than to its suggested descendants (p. 54). Whilst *A. strachani* could not reasonably be placed in *Lagarograptus*, which develops pronounced ventral apertural processes, it could be considered a borderline case for inclusion in *Monoclimacis*, and is in our view a likely forerunner of the early members of that genus (p. 54).

A. gracilis probably represents an early tendency towards gracilization in the monograptid stock. Similar tendencies are seen in most groups, particularly in their early stages of evolution : subsequently tendencies to rhabdosomal robustness are more common (e.g. p. 93).

Atavograptus is one of the most important genera of Silurian graptolites. It is the first monograptid genus, has relatively simple thecae which provide a good basis for subsequent modifications (geniculation, introversion, thecal hooks), and some of its species (e.g. *A. atavus*) are long-ranging and abundant.

22. *Pribylograptus*. Pribylograptids were the first described monograptids with introverted thecae (Rickards & Rushton 1968). Their discovery led to a greater understanding and unravelling of the complex evolution of the slender early Llandovery monograptids in which the roots of the later important genera are located (Hutt & Rickards 1970, Rickards & Hutt 1970). Hutt & Rickards considered it unlikely that *Pribylograptus* could have given rise to other genera than cladia-bearing types (p. 71), but it has been shown by Hutt (1974) that the paired introverted horns can be modified to extroverted thecal hooks (p. 45), a tendency which affects several stocks in the *cyphus* and *triangulatus* Zones (Fig. 17), and the recognition of which in pribylograptids poses several problems with respect to the origin of hooked monograptids (see below).

The early pribylograptids (Fig. 17 ; *P.* cf. *incommodus*, *P. sandersoni*, *P. incommodus*) are very slender species with rather variable flexuous curvature, horned introverted apertures, and with a slight geniculum but lacking a genicular hood. The gentle geniculation reflects their origin from *A. ceryx* : the sicula is only known in *P. argutus* and, as in *A. ceryx*, it is relatively small (1·0 mm). Later pribylograptids (Fig. 17 ; *P. argutus* and subspecies, *P. leptotheca*) have more robust rhabdosomes and *P. argutus* has a stiff dorsal curvature : both possess genicular hoods. The acquirement of genicular hoods in the span of the *triangulatus* to *sedgwickii* Zones is a feature exhibited by several other groups at the same time (*Lagarograptus*, *Monoclimacis*, as well as biserial species). It is also noteworthy that the development of such complex apertural apparatus in pribylograptids can be contrasted with lack of change displayed by the sicula and the proximal end. In those genera (e.g. *Coronograptus*, p. 41) in which great sicular changes take place, there is little or no modification of the thecae or thecal apertures. Almost all monograptid lineages displayed this feature of considerable development of one or two biocharacters with little or no alteration to the rest.

Following the establishment of *P. incommodus* a tendency to gracilization is probably reflected in the minute species *P. angustus* Rickards from the *sedgwickii* and *turriculatus* Zones : this particular tendency to gracile rhabdosomes is unusual in that *P. angustus* is the last known pribylograptid, although a parallel might be drawn here with the last, small, species of several biserial groups of graptoloids. Earlier forms show the same tendency less spectacularly (*P. argutus sequens* Rickards, *P. jonesi* Rickards) but the main trend within the genus is towards quite robust rhabdosomes.

It is possible that pribylograptids are the ancestors of *Barrandeograptus* (p. 72), and almost certain that the *M. sudburiae* group discovered by Hutt derived from *P. argutus* or a like form. Indeed it is possible that many of the records of *P. argutus* are really referable to *M. sudburiae* since both proximal and distal parts are necessary to identify either. Otherwise the bulk of monograptid groups probably originated from *Atavograptus* and not from *Pribylograptus*.

23. *Coronograptus*. The suggested record and evolution of the coronograptids is shown in Fig. 17. The genus, like *Pribylograptus* and *Lagarograptus* (p. 42), has recently been redefined by Rickards (in press) (see also p. 103) and is taken now to include those species which develop elongation of the sicula (particularly) and thecal tubes, display a slight geniculation, but show little change of the thecal apertures except rare isolation. Increase in the thecal length is accompanied by increased thecal overlap (presumably leading to a lessening of the geniculation) and increased dorsoventral width.

C. cyphus praematurus (Toghill) is the earliest recorded species, appearing more or less simultaneously with *A. atavus* in the section at Dobb's Linn. Its origin is certainly within the *atavus* group (its only described uniserial predecessor is *A. ceryx*) and it probably retains, like the other species in the genus, a slight geniculation. The sicula is longer than in *A. ceryx* and the species is best regarded as having originated from the *A. ceryx–A. atavus* lineage at or about the base of the *atavus* Zone. The main change is one of increased thecal length and overlap.

C. c. cyphus, the succeeding coronograptid, is very similar indeed to *C. c. praematurus* in general rhabdosomal characters but the latter is less tightly curved, in which it is intermediate between *Atavograptus* and *C. c. cyphus*, and has a shorter sicula. *C. gregarius*, including the subspecies *C. g. arcuatus* Obut & Sobolevskaya and *C. g. minisculus* Obut & Sobolevskaya, displays a sicula which increases in length up the stratigraphical sequence to a maximum of 12 mm in specimens of *C. g. gregarius* from the *argenteus* Zone of the Lake District. The *gregarius*-like species, in addition to increased sicula length, exhibit occasional isolation of the thecal apertures but the dorsoventral width does not achieve the proportions of *C. cyphus*.

Coronograptus therefore represents a tightly knit low Llandovery genus with unambiguous origins in the *Atavograptus* lineage, and with no traces of subsequent evolution to other genera or groups presumably because of the extreme specialization of the proximal regions. Certainly these species cannot be included in *Pristiograptus* as has been done by some authors (e.g. Strachan 1971) : pristiograptids almost certainly originated in certain *magnus*-Zone derivatives of the *atavus* group (p. 64).

24. *Lagarograptus.* Representatives of this genus first appear in the *acinaces* Zone (Fig. 17) in the form of *L. acinaces* (Pl. 6, fig. 3), a species characterized by a delicate *ventral* apertural process, a flowing geniculum, a thecal excavation and a long sicula. Subsequent species, *L. inexpeditus* Obut & Sobolevskaya and *L. tenuis* (Portlock), show little change in the sicular length and position, but the geniculation increases and a pronounced genicular hood is developed above the more semicircular thecal excavation. The ventral apertural process remains similar, as does the general form of the rhabdosome involving gentle to strong dorsal curvature. It has been shown by Rickards (in press) that the ventral apertural process displays fusellar growth bands, and the presence of such a structure in all the representatives of the genus precludes any obvious connection of it with reproduction (cf. Obut & Sobolevskaya 1968). The genus has been redefined on the bases of the above characters by Rickards (in press), following earlier discoveries by Rickards & Rushton (1968) and Hutt (1968) on the detailed morphology of these and related species groups.

The thecal overlap in *L. acinaces* (Fig. 17) is at least two-thirds, a tendency which affected the *Atavograptus–Coronograptus* lineage at about the same time. The overlap apparently lessened in subsequent coronograptids such as *C. gregarius* and the same may have occurred in the later lagarograptids, although the preservation is not always sufficient to be certain. *Lagarograptus* is morphologically the most compact of groups but has a rather long stratigraphical record (Fig. 17) considering its poor representation at each horizon. The origin of *L. acinaces* almost certainly lies with *A. strachani* which had already developed considerable thecal overlap, a geniculum of similar aspect and a long sicula; it has similar rhabdosomal dimensions.

25. The '*revolutus*' group with simple hooks. As a result of Hutt's work on the type *revolutus* specimens of Kurck, the *sudburiae* group of forms with distal introverted thecae was established (p. 45). The remaining '*revolutus*' types fall into two groups, those with simple thecal hooks and those with hooks composed of paired horns. *M. revolutus austerus* Törnquist is the species next in priority after *M. revolutus revolutus* Kurck (now transferred to the *sudburiae* group) and forms a convenient title for the remaining species which are regarded here as subspecies of *M. austerus.* They may be grouped as follows.

1. Forms with simple hooked proximal thecae or possibly with very slight transverse expansion: *M. austerus austerus* Törnquist, *M. austerus* subsp. A (= *M. revolutus* A of Sudbury, *M. a. vulgaris* Hutt 1974), *M. austerus* subsp. D (= *M. revolutus* D of Sudbury, *M. a. sequens* Hutt 1974), *M. difformis* Törnquist.
2. Forms with proximal hooks composed of paired horns: *M. austerus bicornis* Hutt 1974 (= *M. revolutus* B of Sudbury), *M. austerus praecursor* Elles & Wood (i.e. *M. revolutus praecursor* of Elles & Wood) [for *M. revolutus* C of Sudbury, = *M. sudburiae* Hutt, see p. 45].

Those forms in group 2 are discussed in section 26, p. 44. *M. austerus austerus* is the earliest species of the group, appearing in the *cyphus* Zone, possibly a little earlier than *M. austerus vulgaris* (= subsp. A) and *M. difformis*, both of which occur in the top of the *cyphus* Zone. *M. a. austerus* differs from *M. a. vulgaris* mainly in being less strongly and less regularly dorsally flexed; since Sudbury (1958) has demonstrated that increased dorsal curvature in these forms takes place with time, the distinction may be a real one. Otherwise the two are very similar, with long slender proximal regions comprising at least 25 hooked thecae of low overlap and distal regions with the thecae inclined to the axis at about 15° (Fig. 19).

The only likely ancestors to the *M. austerus* group with simple hooks are in the genus *Atavograptus*. A *Pribylograptus* species close to *P. argutus* almost certainly gave rise to *M. sudburiae* (p. 45), but there is no evidence at all of the considerable changes that would be necessary to derive a form with simple hooks proximally and simple tubes distally from a species with strongly introverted thecae throughout. Therefore we suggest that *M. a. austerus* is derived directly from the earlier

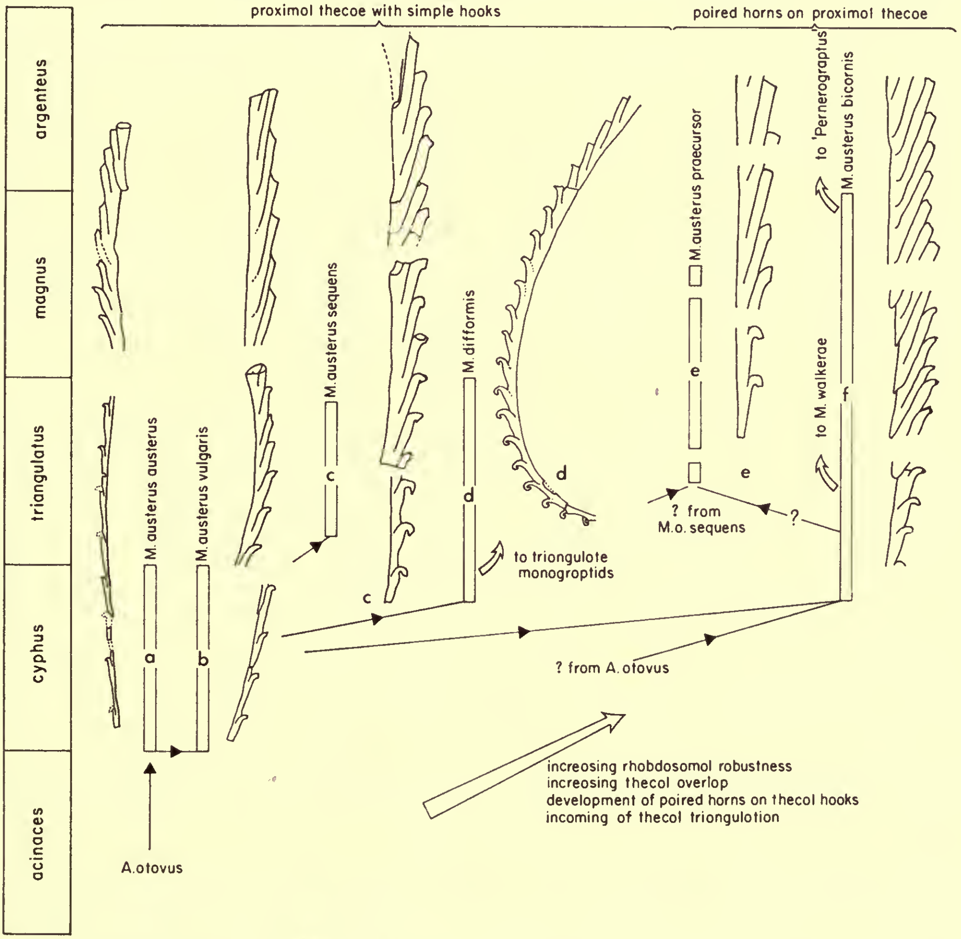

argenteus
magnus
triangulatus
cyphus
acinaces
proximal thecae with simple hooks
paired horns on proximal thecae
M. austerus austerus
M. austerus vulgaris
M. austerus sequens
M. difformis
M. austerus praecursor
to 'Pernerograptus'
M. austerus bicornis
to M. walkerae
a
b
c
c
d
d
e
e
f
to triangulate monograptids
? from M.a. sequens
?
? from A. atavus
A. atavus
increasing rhabdosomal robustness
increasing thecal overlap
development of paired horns on thecal hooks
incoming of thecal triangulation

FIG. 19. Evolution of the *M. austerus* group: a, SM A23923; b, GSM Pg1015; c, SM A24508; d, LO 1470T; e, GSM Pg867; f, SM A24505. All figures ×3½.

A. atavus. Unlike later forms of *M. austerus,* with their greater dorsal curvature, *M. a. austerus* has a rhabdosomal form and dimensions similar to *A. atavus.* This resemblance extends even to the nature of the very long slender proximal region of both species. The only changes necessary in such a lineage would be the growth of simple hooks (Fig. 19) on the proximal thecae – proximal introduction of an apertural modification – and a lessening of the *atavus* geniculum particularly in the distal regions of *M. a. austerus. A. atavus* itself displays less geniculation in its distal thecae. Therefore *M. a. austerus* is considered a probable direct descendant of *A. atavus,* and a certain direct ancestor of the more stiffly curved *M. austerus vulgaris* (Fig. 19).

M. a. vulgaris is followed in the *triangulatus* Zone by *M. a. sequens* (= *M. revolutus* D of Sudbury) which has up to 40 simply hooked thecae, increased thecal overlap (compared with *M. a. vulgaris* where the overlap begins at about th15), an increased dorsoventral and lateral width and increased angle of thecal inclination (20°) : in short it is a more robust species than *M. a. vulgaris* and has more hooked thecae. *M. a. sequens* is found as high as the top of the *triangulatus* Zone in the Rheidol Gorge (horizon C of Sudbury 1958), and is the highest of the *M. austerus* forms with simple hooked thecae.

M. difformis (Fig. 19d) has been shown by Hutt (1974) to appear in the top of the *cyphus* Zone. It is a particularly interesting species in that although clearly belonging to the *austerus* group, it is the earliest species with any triangular thecae. The proximal thecae are axially elongate, the mesial triangular and rather *communis*-like (Fig. 19d) and the distal simple tubes : the change from one type to the next is gradual throughout. The significance of triangular thecae in *M. difformis* is discussed below under sections 28 and 32 (pp. 46 and 52).

26. The '*revolutus*' group with thecal horns. Two forms are known to have proximal thecal hooks composed of paired horns : *M. austerus bicornis* Hutt (= *M. revolutus* B of Sudbury) and *M. a. praecursor* Elles & Wood. The first occurs in the top of the *cyphus* Zone (horizon T of Sudbury 1958) and the second succeeds it in the *triangulatus* Zone. The two are clearly closely related, but *M. a. bicornis* is somewhat more robust with considerably greater thecal overlap and thecal inclination, perhaps suggesting that the two forms originated from a common ancestor by similar processes acting at different rates. Both could have evolved directly from *A. atavus,* a species which extends into the *triangulatus* Zone, but it seems more likely that they have evolved from *M. a. vulgaris* and *M. a. sequens* (Fig. 19) by development of thecal horns from a relatively simple hooked aperture. Interpreted thus it means that apertural horns developed at the top of the *cyphus* Zone in two quite different groups, the *M. sudburiae* group (from *Pribylograptus* ; see Fig. 17 and p. 40) and the *M. austerus* group.

This suggested evolution for the *M. austerus* types differs somewhat from that suggested by Sudbury (1958). In the first place it is necessary to exclude her *M. revolutus* C (i.e. *M. sudburiae*) and group it with *M. revolutus* Kurck *sensu stricto* (p. 45). It is far more likely that these evolved from *Pribylograptus* than from *M. a. vulgaris.* Nor is the origin of *M. limatulus* certain, but it is unlikely to have evolved from a form such as *M. sudburiae* since Hutt (1973) has shown that the tiny proximal thecae have a small, relatively simple hook or hood. This is further discussed on p. 51.

We support Sudbury's (1958) derivation of *M. toernquisti* (= *M. walkerae* nom. nov., see p. 104) from *M. a. bicornis* (= *M. revolutus* B), and the subsequent lineage to *M. pseudoplanus* and *M. planus*. It is of note that the change from *M. pseudoplanus* to *M. planus* through the *convolutus* and *sedgwickii* Zones involves the retreat of the dorsal margin of the thecal aperture and a reduction in the length of the thecal processes (horns to short spines). This is paralleled *at the same time* by the change from *M. sedgwickii* to *M. halli* (p. 49) and the two lineages constitute the only ones which we know of which might be termed regressive. The lineage *M. walkerae* (= *M. toernquisti*) to *M. planus* would, if recent continental practice were followed, require the erection of a new genus to embrace it.

The recognition by two of us (R. B. R. & J. E. H.) that *M. argenteus* has proximal hooks with paired horns suggests that Sudbury's derivation from *M. a. praecursor* may be correct, although she was not aware of paired horns in the latter species and it remains distinctly possible that *M. a. bicornis* is the ancestor of *M. argenteus*. We would derive *M. a. praecursor* from *M. a. bicornis* rather than directly from *M. a. vulgaris*. *M. argenteus* is further discussed on p. 51, and *M. communis* on p. 52.

27. The *sudburiae* group, a new group of biform monograptids. The nature of this group, involving *M. sudburiae* Hutt and *M. revolutus* Kurck *sensu stricto*, has been described by Hutt (1974). It has been shown that the distal thecae in Kurck's type and other material, and in Sudbury's (1958) *M. revolutus* C (= *M. sudburiae*), are strongly *introverted* of the *Pribylograptus* type, that is with paired horns directed dorsolaterally. The proximal thecae in both species have *retroverted hooks*, the change from proximal to distal type involving sympathetic retreat and advance of the dorsal and ventral thecal walls respectively (Fig. 17).

M. sudburiae appears in the *cyphus* Zone of the Lake District and extends into the *magnus* Zone, and therefore has a similar range to the other '*revolutus*' types (sections 25 and 26 above). Only two alternative origins are possible for the group. Either they acquired the distal introverted thecae by distal introduction of the new character upon a '*revolutus*' rhabdosome, or they acquired proximal hooks by proximal introduction upon a *Pribylograptus* rhabdosome. We are strongly in favour of the latter interpretation because the *Pribylograptus* species were already established in the *atavus* Zone, and the tendency to develop 'hooks' (which became strong in the *cyphus* Zone) probably affected *Pribylograptus* just as it affected other groups at the same time. Furthermore, there is no evidence that thecal introversion affected any other groups after its inception through the *Atavograptus–Pribylograptus* lineage.

Thus we suggest that *M. revolutus* Kurck *sensu stricto* and *M. sudburiae* Hutt were derived from the *P. incommodus–P. argutus* lineage at a point probably close to the origin of *P. argutus* (Fig. 17). At present the group includes only the two species, and although we feel its evolutionary roots to be quite clear and its evolutionary potential to have probably been low, we would refrain for the present from creating a new genus to embrace the group.

28. *'Demirastrites'*. The status of *'Demirastrites'* has been discussed by Bulman & Rickards (*in* Bulman 1970): it was erected by Eisel (1912) and has *M. triangulatus* as type species, subsequently designated by Bulman (1929). Continental workers have used the concept to embrace those species which in silhouette have *Rastrites*-like thecae at the proximal end and more or less triangular thecae distally (e.g. Přibyl & Münch 1942). That the evolution is extremely complicated, involving many unsuspected morphological features, has been amply demonstrated by Sudbury (1958). Her evolutionary lineages include forms which are not strictly demirastritid (e.g. *M. triangulatus fimbriatus*).

M. triangulatus appears at the base of the *triangulatus* Zone slightly before the first rastritids and Sudbury has convincingly demonstrated the origin of *R. longispinus* from *M. triangulatus* through intermediate forms such as *M. t. extremus* following an earlier suggestion of Elles (1922). Other rastritids may have evolved from other 'demirastritid' lineages (e.g. *Rastrites peregrinus*) and the genus is almost certainly polyphyletic.

The origin of *M. triangulatus* (Pl. 5, fig. 3) is problematical, for as well as having triangular thecae it has proximal rastritiform (i.e. *isolate*) thecae. We have shown that thecal isolation may take place in other groups at this time (*Coronograptus*, p. 41, and *Monograptus*, p. 44) whilst triangular thecae are present in *M. difformis* at the top of the *cyphus* Zone. Thus the processes necessary to derive *M. triangulatus* were in operation in late *cyphus*-Zone times. Sudbury did not think *M. revolutus* (= *M. austerus* herein, p. 42) to be a likely ancestor for *M. triangulatus* since the former has a great many axially elongate thecae. However, she did not seem aware of the triangular thecae in *M. difformis*. In our view this feature makes *M. difformis* the only (known) likely ancestor to the *M. triangulatus* group and in particular to *M. t. separatus* (Pl. 2, fig. 2); it should be remembered that the triangulates do have one axially elongate theca, namely th1, whilst some have no rastritiform thecae (*M. t. fimbriatus*). Otherwise we strongly support Sudbury's evolutionary suggestions for the triangulate monograptids.

Sudbury suggested four main lineages excepting those known to lead to rastritids. These are: 1, *M. t. fimbratus* (Pl. 5, fig. 6) to *M. t. similis*, leading eventually to *M. spiralis*; 2, *M. t. major* (Pl. 5, fig. 2) to *M. convolutus* (Pl. 5, fig. 1); 3, *M. t. separatus* to *M. denticulatus*; 4, *M. t. separatus* to *M. decipiens*. The first of these lineages involves the loss of newly acquired rastritiform thecae, and the development of thecal spines from thecal horns (Fig. 20), whilst the second and fourth involve increasing numbers of rastriform thecae and the development of rather long, high triangular thecae. The *M. denticulatus* lineage was presumably regarded by Sudbury as a side branch unlikely to produce further species. Indeed the end products of lineages 3 and 4 above, *M. denticulatus* and *M. decipiens*, are species lacking thecal horns but with relatively simple apertures. It may well be that they had their origins independently in the *M. austerus sequens* lineage mentioned above (p. 44).

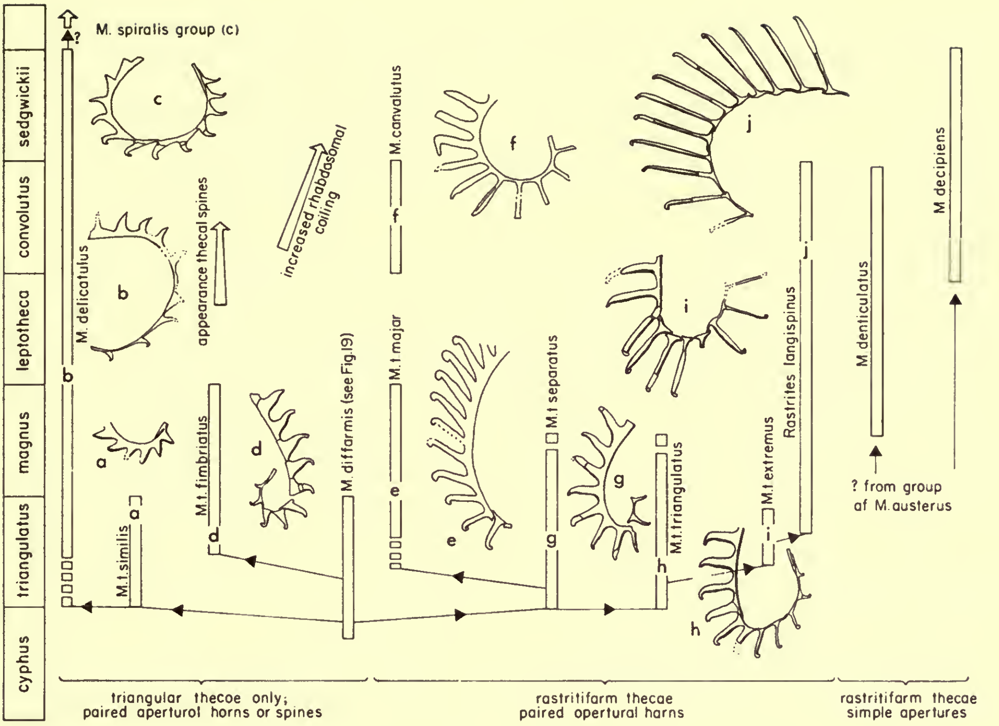

cyphus
triangulatus
magnus
leptotheca
convolutus
sedgwickii
? M. spiralis group (c)
M. delicatulus
a
b
c
M.t.similis
appearance thecal spines
M.t.fimbriatus
d
increased rhabdosomal coiling
M. difformis (see Fig.19)
M.t.major
e
M.convolutus
f
M.t.separatus
g
M.t.triangulatus
h
M.t.extremus
i
Rastrites longispinus
j
M denticulatus
M decipiens
? from group of M.austerus
triangular thecae only; paired apertural horns or spines
rastritiform thecae paired apertural horns
rastritiform thecae simple apertures

FIG. 20. Evolution of the triangulate monograptids (*'Demirastrites'*) and some *Rastrites* : a, SM A21479 ; b, SM A21431 ; c, SM A24499 ; d, SM A24445 ; e, GSM 26326 ; f, SM A21293 ; g, SM A24437 ; h, SM A24460 ; i, SM A24479 ; j, SM A24498. All figures ×3½.

Thus *'Demirastrites'* could be redefined within the framework outlined by Sudbury (1958), although we do not propose to do this here for two reasons. Firstly, there are too many species (e.g. Přibyl & Münch 1942) the detailed morphology of which is unknown : further study of these might reveal unsuspected complications in lineages proposed on present evidence. Secondly, demirastritids are now known up to and including the *griestoniensis* Zone, yet no successful attempt has been made to unravel their origins, or work out their detailed morphology. On the last point we would tentatively suggest that *M. pragensis pragensis* (Přibyl) (*crispus* Zone) might have evolved from *M. pragensis ruzickai* (Přibyl) (*sedgwickii* Zone).

29. *Rastrites*. The origins of two rastritids, *R. longispinus* (Perner) and *R. peregrinus* (Barrande), have been suggested by Sudbury (1958) to be through *M. t. extremus* and *M. t. praedecipiens* respectively. Other rastritids *may* originate from triangulate monograptids, and Schauer (1967) has outlined some evolutionary lineages within the rastritids themselves.

Schauer distinguishes earlier forms of *R. peregrinus* as *R. p. socialis* which appear closer to the base of the *triangulatus* Zone than does *R. longispinus* in the German sequence. This does not, of course, obviate Sudbury's suggested origin of *R. peregrinus* from *M. t. praedecipiens*, indeed it tends to give it more weight in that it closes the gap in the record present in the Rheidol section. Presumably *R. p. peregrinus* in the sense of Schauer (*convolutus* Zone) evolved directly from the earlier subspecies, and then gave rise to *R.* cf. *p. peregrinus* and *R. perfectus* Přibyl. Further, *R. hybridus* and *R. h. gracilis* may have evolved from *R.* cf. *p. peregrinus* through the morphologically intermediate *R.* cf. *hybridus*, or possibly from *R. h.* subsp. of Hutt (1975).

Further lineages within the rastritids will have to be worked out following careful studies in different regions of the actual ranges of the species, as well as of their detailed morphology which in many species is but poorly understood. At present it can be stated that following the *R. longispinus* and *R. peregrinus* lineages initiated in the *triangulatus* Zone there are at least two differing groups in the *convolutus* Zone, the *R. approximatus* Perner and the *R. richteri* Perner. The latter has thecae and a rhabdosomal form very similar to *M. denticulatus* (*magnus* to *convolutus* Zones) and may well have evolved from this species. *R. approximatus* Perner, *R. phleoides* Törnquist (*convolutus* Zone) and *R. rastrum* (Richter) (*sedgwickii* Zone) have thecae of the proximal *convolutus* type, even to the presence of pronounced, paired, apertural processes in *R. a. geinitzi* Törnquist and *R. phleoides* : the group may well be related to *M. convolutus*, a 'demirastritid'.

R. spina, *sensu* Schauer (1967), (*sedgwickii* Zone) is of *R. fugax* Barrande type ; it may thus form a link with what Schauer terms the *R. linnaei* Barrande group which typifies the lowest parts of the *turriculatus* Zone and which included *R. linnaei*, *R. maximus* Carruthers, *R. carnicus* Seelmeier, *R. distans* and *R. fugax*. *R. spina*, *sensu* Rickards (1970) and Hutt (1975), is quite different from Schauer's form (Fig. 21) and may well have evolved directly from a monograptid such as *M.* sp. Hutt (Fig. 21) which ranges from the *magnus* at least into the *turriculatus* Zone. *M.* sp. is discussed in more detail on p. 58, but in essence is a *Monograptus* s.s. with isolate proximal thecae and more triangular distal thecae : a 'demirastritid' in the genus *Monograptus*.

Detailed morphological studies may well show that some of the suggested lineages are untenable. In few cases is the nature of the thecal hook in rastritids known. Hutt *et al.* (1970) established that the hook in *R. linnaei* was a rather simplified version of the paired horn triangulate monograptid structure, in which the dorsal margin and the horns themselves had retreated somewhat. Earlier species such as *R. longispinus* have quite pronounced horns, whilst others have extremely long apertural spines perhaps resulting from drawn-out horns (e.g. *R. phleoides*, Fig. 21). It is of great interest that the spinose rastritids reached their acme in the *convolutus* and *sedgwickii* Zones at exactly the same time as spinose 'demirastritids' and spinose monograptids of the *sedgwickii* type and thereafter the dorsal wall of the thecal tube retreated, as it also did in the latter groups.

30. *Monograptus sedgwickii*. Elles (1922) placed *M. sedgwickii* Portlock (Pl. 5, fig. 5) in an intermediate position in a lineage leading from *M. clingani* Carruthers to *M. marri* Perner (Pl. 6, fig. 2) and hence to the *M. priodon* Bronn

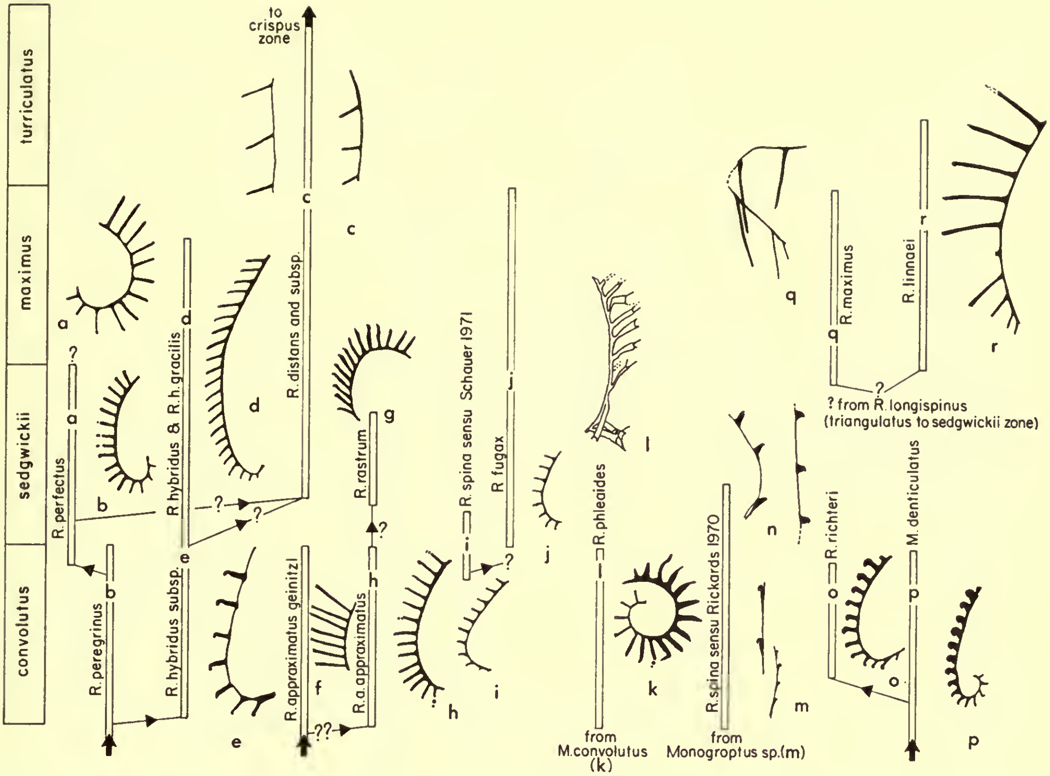
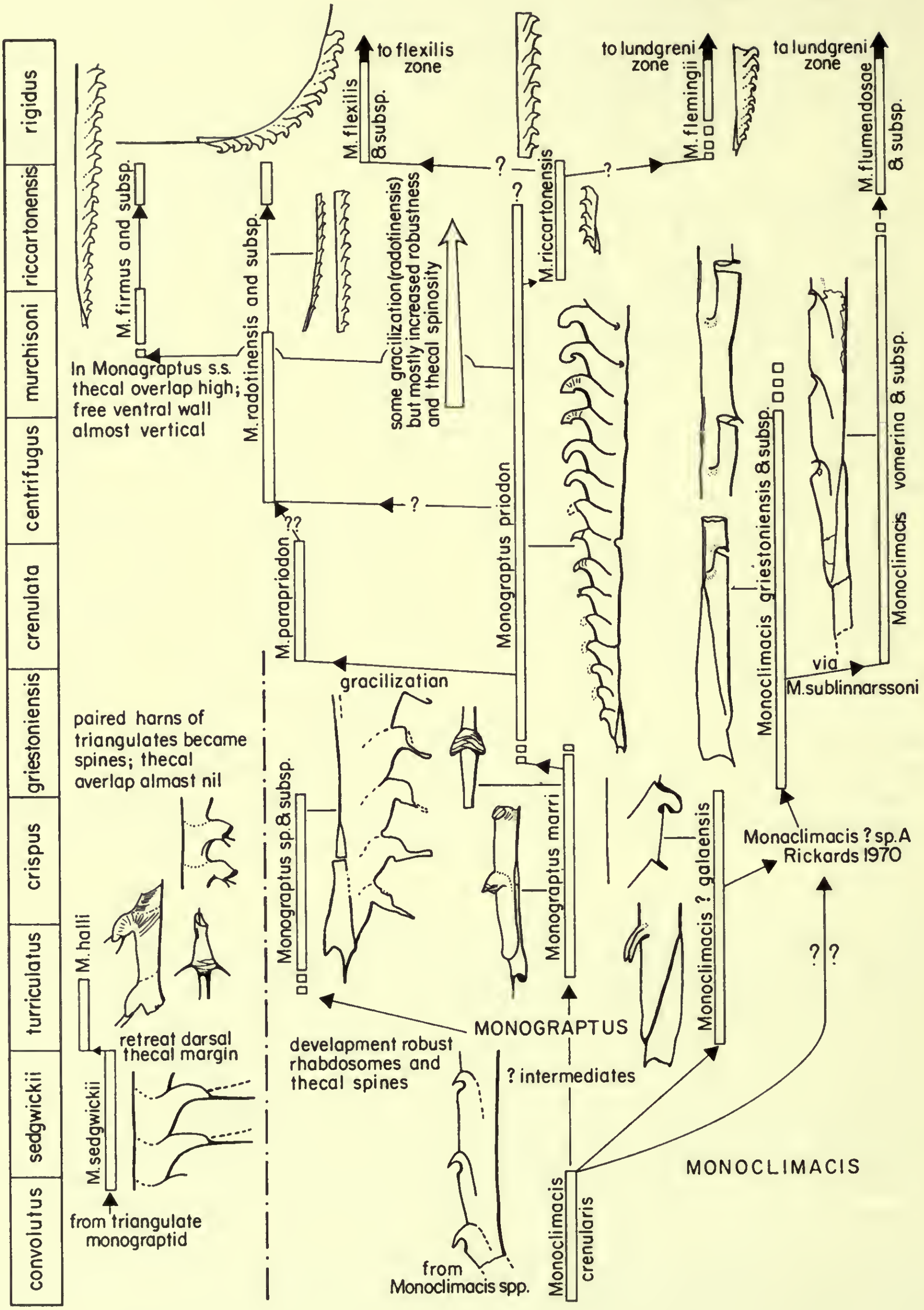

turriculatus
maximus
sedgwickii
convolutus
to crispus zone
R. perfectus
R. peregrinus
R. hybridus & R. h. gracilis
R. hybridus subsp.
R. distans and subsp.
R. approximatus geinitzi
R. a. approximatus
R. rastrum
R. spina sensu Schauer 1971
R. fugax
R. phleoides
R. spina sensu Rickards 1970
R. maximus
R. linnaei
? from R. longispinus (triangulatus to sedgwickii zone)
R. richteri
M. denticulatus
from M. convolutus (k)
from Monograptus sp. (m)
a
b
c
d
e
f
g
h
i
j
k
l
m
n
o
p
q
r
?
??

FIG. 21. Evolution of *Rastrites*: a, b, d, f, g, h, i, j, after Schauer (1967); c, LU 57755 and HUR S197,5.5/11; e, LU 57747; k, SM A21293; l, LU 57751; m, LU 57669 and LU 57670; n, HUR 9Wa/45 and LU 57752; o, after Schauer (1967); p, BM(NH) Q96; q, HUR S123,7.25/19; r, HUR S136,1.25/2. All figures ×1¾, except k, ×¾ approx., and e, m, and n, ×3½. Note suggestion of several possible ancestors for rastritids.

plexus. Whilst few workers would now relate *M. sedgwickii* in any way to *M. clingani* the idea became firmly established that the former was a forerunner of the *priodon* lineages. However, Hutt *et al.* (1970), working on isolated specimens of *M. halli*, deduced that it and probably *M. sedgwickii* were more likely to have originated from a triangulate monograptid and that the undisputed *sedgwickii–halli* lineage was unlikely to have given rise to later monograptids. The thecae in both *sedgwickii* and *halli* show no overlap and are essentially triangular in nature. *M. sedgwickii* has uniform thecae whilst *M. halli* has *sedgwickii*-like thecae at the proximal end but a ventrally facing aperture and short spines on the distal thecae. The great similarity between the *sedgwickii* thecal type and that of triangulate monograptids is illustrated in Fig. 22. The main problem concerning the origin of *M. sedgwickii* – it appears rarely at the top of the *convolutus* Zone – is in finding an ancestor which could give rise to the characteristic *sedgwickii* proximal end superficially resembling that in the *priodon* group (Fig. 22). Perhaps the most likely


rigidus
riccartonensis
murchisoni
centrifugus
crenulata
griestoniensis
crispus
turriculatus
sedgwickii
convolutus
M.firmus and subsp.
In Monograptus s.s. thecal overlap high; free ventral wall almost vertical
M.radotinensis and subsp.
to flexilis zone
M.flexilis & subsp.
some gracilization (radotinensis) but mostly increased robustness and thecal spinosity
?
Monograptus priodon
M.riccartonensis
to lundgreni zone
M.flemingii
to lundgreni zone
M.flumendosae & subsp.
Monoclimacis vomerina & subsp.
Monoclimacis griestoniensis & subsp.
via M.sublinnarssoni
??
M.parapriodon
gracilization
paired horns of triangulates became spines; thecal overlap almost nil
M.halli
retreat dorsal thecal margin
M.sedgwickii
from triangulate monograptid
Monograptus sp. & subsp.
Monograptus marri
MONOGRAPTUS
development robust rhabdosomes and thecal spines
? intermediates
from Monoclimacis spp.
Monoclimacis ? galaensis
Monoclimacis ? sp.A Rickards 1970
??
MONOCLIMACIS
Monoclimacis crenularis

ancestor is in the *M. walkerae* (= *M. toernquisti* Sudbury) group. In this group Sudbury (1958) has shown that the slender proximal region with tiny axially elongate thecae is progressively reduced in stratigraphically higher horizons to give rise to species like *M. pseudoplanus* and *M. planus*. This lineage, like the *sedgwickii–halli* line, also exhibits retreat of the dorsal margin of the thecal tube and reduction of the horns or spines. Thus the *pseudoplanus–planus* line could have evolved *M. sedgwickii* by further, but not complete, straightening of the proximal end and the development of long spines from the paired horns of *M. pseudoplanus*.

31. '*Pernerograptus*'. *M. argenteus* Nicholson is the type species of *Pernerograptus*, a name given by Přibyl (1941) to embrace Elles & Wood's (1901–18) Group IB 1. Bulman (1951) subsequently redescribed the thecae of *M. argenteus* and interpreted them from three-dimensional pyritized specimens as having relatively simple hooks. We have examined many topotypes in three dimensions, and are of the opinion that the thecal hook exhibits the paired horn structures first detected in triangulate monograptids by Sudbury (1958). Thus *M. argenteus* may have evolved from *M. austerus praecursor* as Sudbury suggested, or from *M. a. bicornis* as we suggest. Sudbury was unaware of the paired horn structure exhibited by the thecae of *M. a. praecursor*.

Hutt (1975) has shown that *M. argenteus cygneus* Törnquist is a junior synonym of *M. a. argenteus*, a fact long suspected by some workers (e.g. Rickards 1970), whilst *M. limatulus* Törnquist has tiny proximal thecae with small hood-like hooks quite unlike the horns of *M. argenteus*. The number of species which can be grouped with *M. argenteus* in *Pernerograptus* thus dwindles considerably. The evolutionary relationships suggested above for the *M. austerus* forms with paired horn structures (pp. 42–44) indicate that *M. argenteus* can only reasonably be grouped with *M. a. praecursor* and with *M. a. bicornis*, and that *Pernerograptus* must be restricted to these two species. Some doubts are thus cast upon its utility. Almost certainly future work will show that *M. a. praecursor* and *M. a. bicornis* will have to be raised to specific status to distinguish them from *M. a. austerus* and the simple hook lineage (Fig. 19). We are uncertain of the morphology of *Pernerograptus sidjachenkoi* Obut & Sobolevskaya (1966) from the *convolutus* Zone, and *Pernerograptus omulevkaensis* Obut (1965) from about the *triangulatus* Zone.

FIG. 22. Evolution of *M. sedgwickii* and Llandovery and Wenlock *Monograptus* s.s.: *M. sedgwickii* idealized distal thecae, ×9; *M. halli*, Riksmuseum Cn 54941 and Cn 54942, ×9 and ×4½; *Monoclimacis crenularis*, on same slab as BU 1564b, ×13½ approx.; *Monograptus* sp., GSM R56579, ×13½ approx.; *M. marri*, Riksmuseum Cn 54937 and Cn 54938, ×13½ approx.; *Monoclimacis ? galaensis*, reconstruction of near proximal thecae, and proximal end with sicula, BU 1569, ×13½ approx.; *Monograptus priodon*, GSM BAH1082, ×3½ approx.; *Monoclimacis griestoniensis*, on same slab as SM A21681, ×22½; *M. vomerina vikensis*, SM A62903, ×13½ approx.; *Monograptus firmus*, HUR 40W/1, ×2¼; *M. radotinensis inclinatus*, HUR 39W/3, ×2¼; *M. riccartonensis*, BU 1586 and BU 1587, ×2¼; *M. flexilis*, SM A22317, ×2¼; *M. flemingii*, BU 1581, ×2¼.

32. *'Campograptus'*. This was established by Obut (1949) with *M. communis* as type species, and originally defined as a dorsally curved monograptid with hooked thecae greatly expanded at their bases. Such a definition is untenable on present knowledge, and it was left to Bulman (1951) and Sudbury (1958) to illustrate the thecal structure. The nature of the thecal hook is known only in the type species (*M. c. communis* Lapworth, *M. c. rostratus* Elles & Wood and *M. c. obtusus* Rickards) where it consists of a relatively simple open hook (Fig. 23) in which both ventral and dorsal thecal walls take part : the lateral part of the apertural lip is slightly convex (Sudbury 1958 : pl. 23, fig. 100).

Sudbury suggested an evolutionary lineage of *M. communis* from *M. revolutus praecursor* (= *M. austerus praecursor* herein) and whilst we point out (p. 42) that the latter has paired thecal horns, the superficially similar coeval species *M. austerus* subsp. A (= *M. revolutus* A of Sudbury) has simple hooked thecae ; we suggest it as the only likely forerunner of *M. communis*.

Subsequently development of the *M. communis* line involved the loss of two proximal axially elongate thecae to result in *M. c. rostratus* (Sudbury 1958), whilst Rickards (1970) indicated that *M. c. obtusus* from the *sedgwickii* Zone might be a later stage of the same trend in which all the axially elongate thecae had been lost. Should then *M. millipeda* (*argenteus* Zone) and *M. clingani* (*convolutus* Zone) be referred to *Campograptus*? They have no axially elongate thecae but are uniform monograptids with a basic *communis*-like thecal tube. The hooked part of the metatheca in *M. millipeda* occupies a much greater proportion of the thecal tube than in *M. communis*, whilst the aperture itself faces the dorsal side of the rhabdosome. That is, the larger hook is more enrolled than in *M. communis* (Fig. 23). However, the hook itself seems to be of simple type and there is a suggestion of slight convexity of the lateral apertural walls as in *M. communis*.

M. millipeda is perhaps best regarded as an offshoot from the *M. communis* lineage in which the processes leading to *M. c. rostratus* have taken place more fully. Considered thus *M. c. obtusus* could have evolved either from *M. c. communis* or from *M. millipeda*. The former seems a more likely ancestor since the hook in *M. millipeda* is already much more tightly enrolled than in the later *M. c. obtusus*. In any event *M. millipeda* seems a likely candidate for a redefined *Campograptus*.

M. clingani (Pl. 4, fig. 3) should probably also be included in a redefined *Campograptus*, although the nature of the thecal hook is less certain than in *M. millipeda* and general rhabdosomal form is as a rule little better than a rough guide (p. 86). We are uncertain of the position in this scheme of *C. elegans* Koren', whilst *C. curtus* Obut & Sobolevskaya (*in* Obut, Sobolevskaya & Merkuryeva 1968) has been placed in synonymy with *M. millipeda* by Hutt (1975).

It has been suggested above (p. 49) that *Rastrites richteri* might well have evolved from *M. denticulatus* by loss of the mesial and distal thecal type. A further point about *M. denticulatus* is that the distal thecae resemble the thecae of *M. millipeda* which occurs in the preceding zone. The tendency to produce rastritiform proximal ends at these levels applied to *M. millipeda* or *M. communis* would certainly result in a form very close to *M. denticulatus* (Fig. 23). Hutt (1975), however, has recently recorded *M. denticulatus* from the *magnus* Zone. The possibility of a single lineage

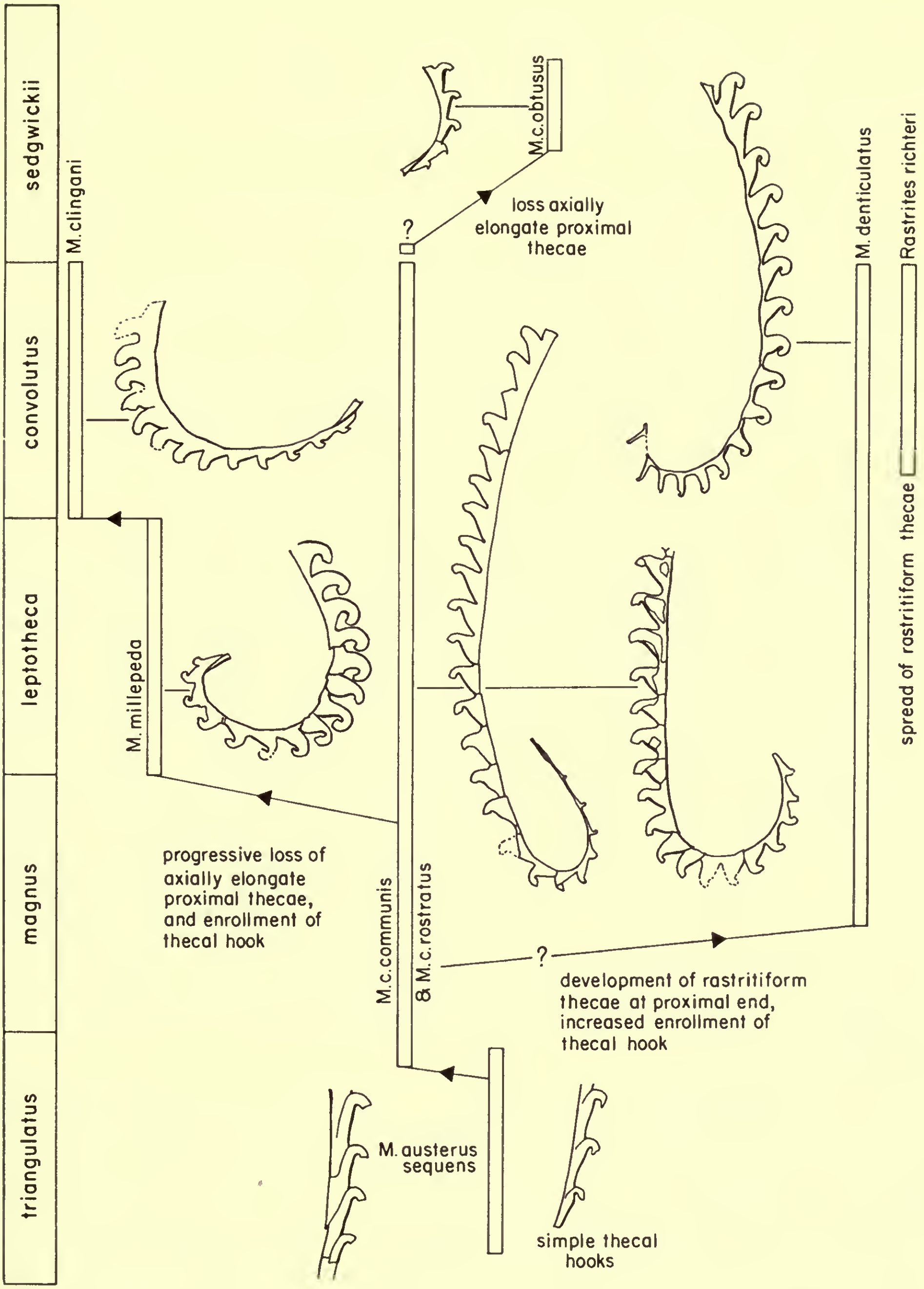

sedgwickii
convolutus
leptotheca
magnus
triangulatus
M. clingani
M. millepeda
M.c.obtusus
?
loss axially elongate proximal thecae
M. denticulatus
Rastrites richteri
spread of rastritiform thecae
progressive loss of axially elongate proximal thecae, and enrollment of thecal hook
M.c.communis
& M.c.rostratus
?
development of rastritiform thecae at proximal end, increased enrollment of thecal hook
M. austerus sequens
simple thecal hooks

FIG. 23. Evolution of the *M. communis* group ('*Campograptus*') : *M. austerus sequens*, SM A24508 ; *M. c. communis* and *M. c. rostratus*, respectively SM A24487 and SM A24493 ; *M. denticulatus*, SM A21418a ; *M. millipeda*, LU 57684 ; *M. clingani*, LU 57688 ; *M. communis obtusus*, HUR S80,8.4/90. All figures × 4½.

evolving from '*Pernerograptus*' *austerus sequens*, to '*Campograptus*' *communis*, to '*Campograptus*' ? *millipeda*, to '*Demirastrites*' *denticulatus*, to *Rastrites richteri* (Fig. 23) emphasizes our disquiet about this system of generic classification which blindly ignores the problems of polyphyletic relationships, and is one of the reasons for our reluctance to accept the usefulness of '*Campograptus*' among others.

33. *Monoclimacis* is one of the more important upper Llandovery to low Wenlock genera, but its roots are undoubtedly in the middle to low Llandovery. Preceding the certain monoclimacids, such as *M. griestoniensis*, *M. crenulata* (Pl. 6, fig. 4) and *M. vomerina* at the top of the Llandovery, are the relatively less common species *M.* ? *galaensis* Lapworth (*turriculatus* and *crispus* Zones) and *M. crenularis* Lapworth (*convolutus* Zone). Both species have been re-examined by Rickards (1968), who interpreted the former as basically a monoclimacid but with paired, lateral lappets at the apertures. The lappets are more elongate on the proximal thecae, and in profile often look like simple hooks. Specimens of *M. crenularis* are usually less well preserved, but the thecae have a pronounced geniculum, more or less vertical supragenicular walls, and the proximal thecae at least have some form of 'hook'. The 'hook' *may* consist of a combination of apertural eversion and a genicular hood. Quite well preserved pyritized specimens have recently been collected from the Lake District (Hutt 1975) and whilst these show the monoclimacid thecal tube and geniculum quite clearly, the nature of the 'hook' itself remains somewhat obscure. The distal thecae on this material undoubtedly possess a genicular hood.

A monoclimacid close to *M. crenularis* has recently been obtained from the *argenteus* Zone of the Lake District (Hutt 1975). This form differs from *M. crenularis* in being rather more slender and in having more widely spaced thecae, but the proximal thecae are 'hooked' and distal thecae have a clear geniculum, genicular hood and vertical supragenicular wall. The species is quite close in rhabdosomal dimensions, shape, thecal spacing and structure of thecae (excluding 'hooks' and hoods) to *Atavograptus strachani* Hutt & Rickards (1970), which occurs in the *acinaces*, *cyphus*, and possibly *triangulatus* Zones. We therefore propose the following lineage leading to *Monoclimacis crenularis* – *A. praestrachani*, to *A. strachani*, to *Monoclimacis* sp., to *M. crenularis*. The evidence is that *M. crenularis* Lapworth and its immediate ancestor should be regarded as true monoclimacids.

Subsequent evolution within *Monoclimacis*, prior to the *vomerina* group, is difficult to unravel partly because the basic thecal form of *M.* ? *galaensis* closely resembles that of the *Monograptus marri*–*M. priodon* lineage, and partly because the record of monoclimacids prior to the *griestoniensis* Zone is so poor. The possible link with *Monograptus* s.s. is discussed further below, p. 60. There are probably undescribed monoclimacids in pre-*griestoniensis* Zone strata, and a few have been described and left under open nomenclature (e.g. *M.* ? sp. A of Rickards 1970).

From the *griestoniensis* Zone upwards to the middle Wenlock monoclimacids are well represented by numerous species which fall naturally into two groups, a slender one based upon *M. griestoniensis* and a robust upon the type species of the genus, *M. vomerina*. The detailed evolution of the whole plexus is being studied at

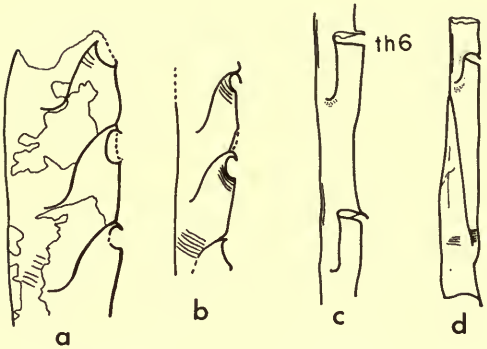


FIG. 24. a, b, *Monoclimacis* of *vomerina* group, GSM PW226, proximal and distal portions of same specimen showing pronounced thecal apertural eversion beneath a genicular hood, × 12½; c, d, *M. griestoniensis*, on same slab as SM A21681, the specimen figured by Elles & Wood (1901–18 : text-fig. 279b), × 25.

present by one of us (R. B. R.), but it can be said that the main difficulty with monoclimacids has been in working out their morphology. Rickards & Smyth (1968) concluded that the genicular hood in *M. flumendosae* (Gortani) was composed of microfusellar tissue, and this has been confirmed from isolated material. But it is distinctly possible (Fig. 24) that the hood in other species consists of excessive growth of the dorsal thecal wall relative to that of the ventral wall. In many, if not most, monoclimacid species the thecal apertures are strongly everted and are almost always overhung by a genicular hood of some kind, particularly in the proximal thecae. The genicular hood of the proximal thecae may be so strongly developed that in profile it may have almost the appearance of a *priodon*-like hood. This fact coupled with the generally similar prothecal proportions and thecal overlap occasionally makes the distinction between *Monograptus* s.s. and *Monoclimacis* s.s. quite difficult.

Urbanek (1958) described *Monoclimacis micropoma* (Jaekel) from the Ludlow, and was the first, in fact, to elucidate the microfusellar hood structure in monograptids (first detected in *Gothograptus nassa* by Holm 1890). In the *lundgreni* Zone of the Wenlock only one monoclimacid is known (*M. flumendosae*) and this differs from all the earlier species in having a flowing geniculum and not quite vertical supragenicular wall. The general form of this species is so unlike *M. micropoma* that it seems unlikely that it has given rise to the latter, and the possibility exists that Ludlow monoclimacids have arisen independently. Mihailova (personal communication) has presumably reached this conclusion in designating some Ludlow species as *Pseudomonoclimacis*. It is exceedingly difficult to make a morphological distinction between Ludlow monoclimacids and those from the Llandovery and Wenlock, or to suggest potential ancestors other than the Ludlow save-all genus *Pristiograptus*. When the range in variation in thecal form in *P. haupti*, which includes some development of a geniculum in the thecae in some specimens (Urbanek 1958), is considered, it might be regarded as a possible ancestor.

34. *Monograptus* s.s. (including *Mediograptus*). A theoretical derivation of *Monograptus* s.s. is easily achieved by spread of the simple hooked thecae of the *M. austerus* group throughout the length of the rhabdosome, but until recently there were very few likely contenders at the right horizons of *triangulatus* to *convolutus* Zones. Prior to the *magnus* Zone no forms referable to *Monograptus* s.s. have been recorded.

The earliest form of which we are aware is a specimen collected by Dr H. Jaeger in 1966 from the Dobb's Linn section at about the level of the *magnus* Zone (top of the *gregarius* Zone as defined by Toghill 1968b : *D. magnus* has since been recorded from the same horizon). This is illustrated in Fig. 25 as *Monograptus* s.s. sp. A. The 67 mm long specimen has hooked thecae throughout the length of the rhabdosome, but otherwise resembles the *M. austerus* group species in all features of rhabdosome size, shape, thecal spacing and basic structure of the prothecal tube. The thecal hooks are seen to be constructed by excessive growth of the dorsal margin relative to the ventral wall, and the ventral lip of the theca is clearly visible beneath the retroverted dorsal wall. Fusellar structure has been detected on the hooks, which do not retreat on the distal thecae. There is little or no sign of transverse expansion. The hook, therefore, differs from the later *priodon* type in that the ventral thecal wall takes no part in it. If, hypothetically, the retroverted dorsal wall were removed from the distal thecae, the remaining rhabdosome would closely resemble *M. austerus*. If all the hooks were removed it would be close to *A. atavus* except that the sicula is too small.

The next similar species of which the authors are aware is *M. undulatus* Elles & Wood (*convolutus* Zone). This has closely similar rhabdosome shape, size and thecal dimensions, and like *Monograptus* sp. A may have thecal overlap of up to one-third. Elles & Wood (1901–18) noted the similarity of the proximal end to that of *M. sedgwickii*, and *M. undulatus* is certainly a possible ancestor of that

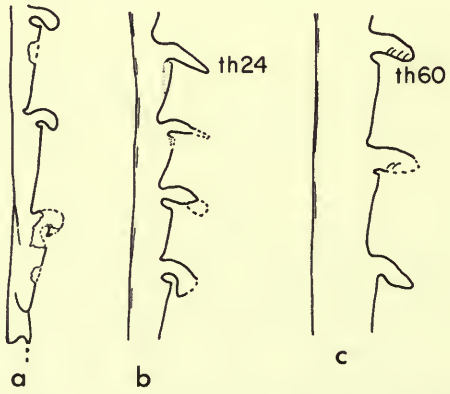


Fig. 25. a–c, *Monograptus* sp. A, proximal, mesial and distal thecae of same specimen, SM A89948, × 25, showing basic *atavus*-like appearance but with strong hooks and hoods composed of fusellar tissue : hypothetical removal of these hoods results in a form very similar to *A. atavus*. Horizon is top of *gregarius* Zone, Dobb's Linn.

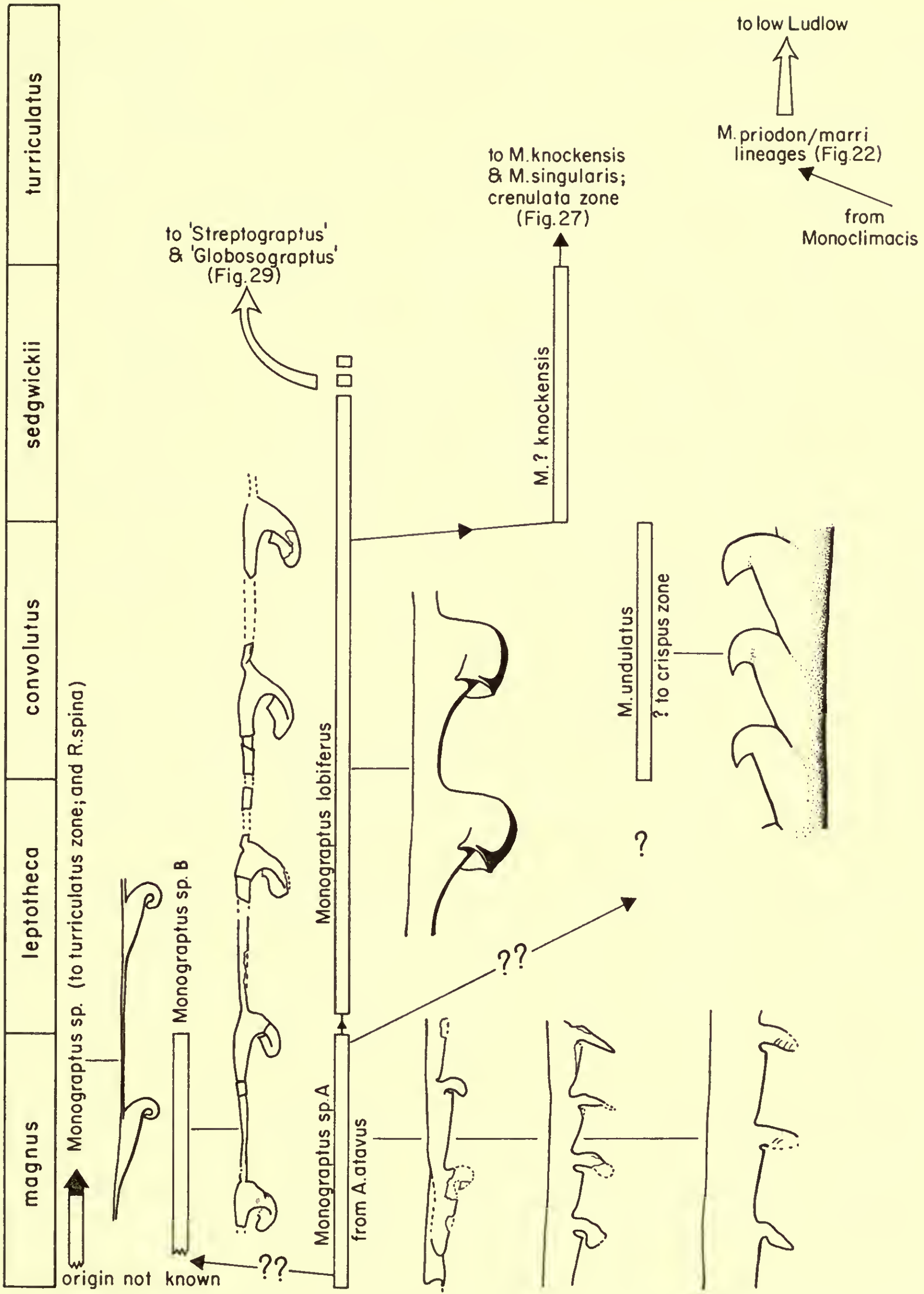

to low Ludlow
M. priodon/marri lineages (Fig. 22)
from Monoclimacis
to M. knockensis & M. singularis; crenulata zone (Fig. 27)
to 'Streptograptus' & 'Globosograptus' (Fig. 29)
turriculatus
sedgwickii
convolutus
leptotheca
magnus
Monograptus sp. (to turriculatus zone; and R. spina)
origin not known
Monograptus sp. B
??
Monograptus sp. A
from A. atavus
Monograptus lobiferus
M.? knockensis
M. undulatus
? to crispus zone
?
??

Fig. 26. Evolution of lobate monograptids : *Monograptus* sp. A. as in Fig. 25 (opposite) ; *Monograptus* sp. with enrolled metathecae, LU 57782 ; *Monograptus* sp. with isolated metathecae, HUR S73,9.4/79 ; *M. lobiferus*, idealized after Bulman (1970) ; *M. undulatus*, GSM 26309. All figures × 22½.

species. However, we prefer to suggest a derivation of *M. sedgwickii* from a triangulate monograptid, thus obviating the need to reduce thecal overlap to nil without change of rhabdosome shape to help the process. The thecal hook in *M. undulatus* appears to involve mostly growth of the dorsal thecal wall.

It might be thought, therefore, that at this level in the Llandovery the potential existed for derivation of, say, the *M. lobiferus* types and the *M. priodon* types. But the position has been complicated by the discovery in the *magnus* Zone of the Lake District of the lobate species *Monograptus* sp. B (Fig. 26) and of *M.* sp. Hutt (Fig. 26). Both are uniform monograptids, the former resembling later derivatives of the *M. lobiferus* group and the latter being unique in its isolation of apparently *Monograptus* s.s. hooks. Thus there are three apparently unrelated *Monograptus* species already present in the *magnus* Zone but as yet no records below this level. All three are slender species and it is quite possible that there are undescribed, slender, uniform *Monograptus* species with thecal hooks in the *triangulatus* Zone.

M. sp. is a species possibly derived from the triangulate monograptids, or from the *M. austerus–M. communis* lineage, by isolation of the proximal type of axially elongate thecae. In view of the simple *priodon*-like hooks, that is with both dorsal and ventral thecal walls participating and lack of thecal horns, the second possibility seems more likely. The axially elongate thecae of *M. communis* are not unlike the distal thecae of *M.* sp., which certainly suggest that thecal isolation is a proximally introduced character as it is in all other known cases.

Monograptus sp. B (Fig. 26) is a very early example of what is commonly achieved at higher horizons in the *lobiferus* group (below), in that both ventral and dorsal thecal walls form a pronounced hook, and then at least the dorsal wall turns proximally and finally dorsally, resulting in a dorsally-facing tube closely adpressed to the ventrally-facing early metatheca. The origin of this form must remain in great doubt, the best that can be said being that it is an early offshoot from the *M.* sp. A–*M. lobiferus* lineage.

There can be little doubt that the lineage *Monograptus* sp. A (*magnus* Zone) to *M. undulatus* (*convolutus* Zone) led to *M. lobiferus* M'Coy (Pl. 5, fig. 4), probably as early as the *argenteus* Zone or at the latest by the base of the *convolutus* Zone. It is possible that the Rickards (1970) records of *M. lobiferus* from the *argenteus* Zone should be referred to *M. millipeda*. *M. lobiferus* differs from *M. undulatus* in being a more robust graptolite in which the lobed effect created by excessive growth of the dorsal thecal wall has become more marked (Fig. 26). It is now known that *M. lobiferus* also has apertural tube-like processes developed from the dorsolateral margins of the aperture (Fig. 27) and directed lateroventrally. Such a structure poses some problems for the apparently obvious sequence of successors to *M. lobiferus*, namely *Monograptus ? knockensis* Rickards (1970), *M. knockensis* Elles & Wood and *M. singularis* Manck. As has been pointed out above, the problematical *M.* sp. B is the earliest known case of thecal lobation, but the trend towards acquiring thecal lobes of some kind in several groups really began at about the level of the *sedgwickii* Zone with *M. ? knockensis* (*sensu* Rickards 1970). This trend was followed shortly after by the acquisition of prothecal folds in different groups.

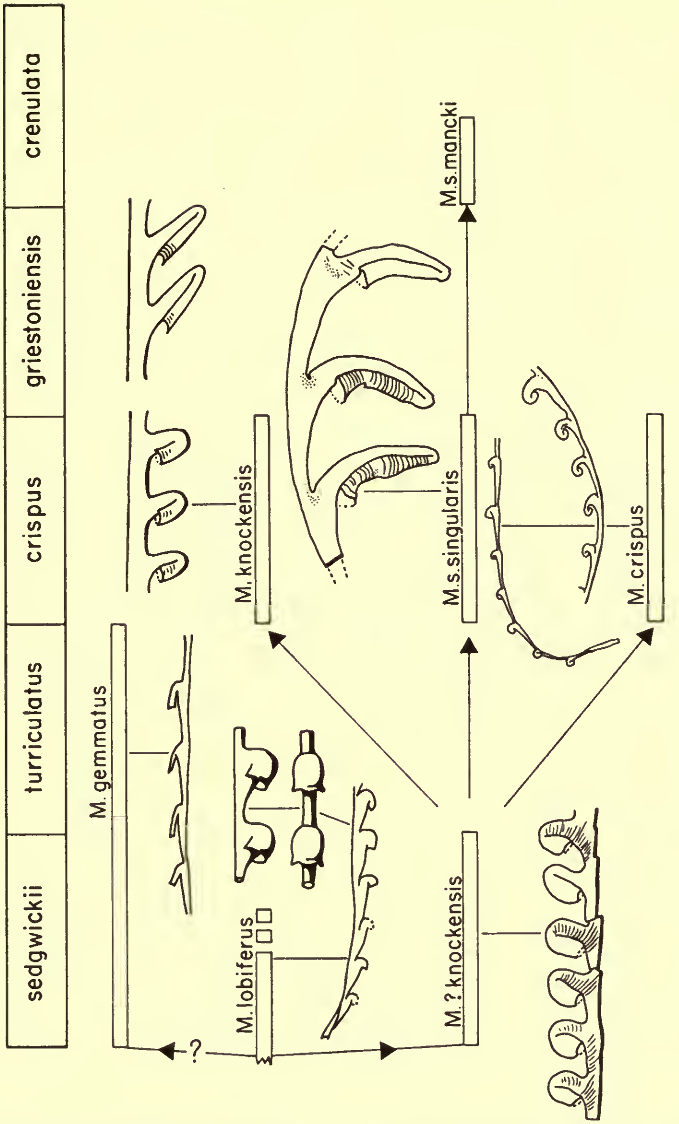

sedgwickii
turriculatus
crispus
griestoniensis
crenulata
M. gemmatus
M. lobiferus
M. ? knockensis
M. knockensis
M.s.singularis
M.s.mancki
M. crispus
?

FIG. 27. Evolution of *knockensis* group of lobate monograptids: *M. lobiferus*, idealized after Bulman (1970) and LU 57720, × 12½; *M. gemmatus*, HUR S94,5.4/40, × 5; *M. ? knockensis*, HUR S80,8.4/144, × 5; *M. knockensis*, SM A21974, proximal and distal thecae, × 5; *M. singularis*, LO 10131T, × 12½; *M. crispus*, BU 1650 and Belfast Natural History Museum figured Elles & Wood (1909–18 : text-fig. 314b), × 5.

The possible links of the *lobiferus*, *knockensis* and *priodon* lines of evolution with such 'genera' as *Globosograptus*, *Streptograptus* and *Mediograptus* is discussed below, but it is necessary first to examine the possible origins of the *priodon* line of evolution which becomes increasingly important from the *turriculatus* Zone upwards into the Wenlock.

M. marri Perner (Pl. 6, fig. 2), commonly regarded as the immediate ancestor of *M. priodon* (e.g. Elles 1922) first appears in the upper third of the *turriculatus* Zone, that is well above the *R. maximus* Subzone and the *M. halli* horizons. The thecal structure has been recently described from isolated material by Hutt *et al.* (1970), where it is seen that as in *M. lobiferus* the hook has a pair of ventrolaterally directed open tube-like processes. However, the thecal hook is not lobed in the extreme manner of *M. lobiferus* and the ventral thecal wall also takes part in the hook (Fig. 22). Therefore if *M. marri* evolved from *M. lobiferus*, ignoring for the moment the unbridged gap of at least the *maximus* Subzone, it would have to be by a pronounced retreat of the dorsal wall of the thecal tube, coupled with *advance* of the ventral wall. The process does occur, partially, in other groups (e.g. the *sedgwickii–halli* line) at this time, but it would have to be reversed in the later *marri–priodon* development.

There is, however, a more satisfactory alternative origin for *M. marri*, namely from the *Monoclimacis* stock, the *crenularis–galaensis* line. Unlike *M. lobiferus* this line has rhabdosomes of exactly the same size and shape as *M. marri* but lacking the thecal hooks. Instead they have genicular hoods and paired lappets. The simple process of coalescence of these lappets dorsally would produce a *priodon*-like thecal hook. The coalescence of lappets to produce hooks has already been detected in the astogeny of *Cyrtograptus* and, indeed, may yet be proved in *M. galaensis* or *M. crenularis*. Further, the hook of *M. marri* displays two features which *Cyrtograptus rigidus* thecal hooks also show, namely a median indentation of the dorsal lip where coalescence takes place along the zigzag line, and ventrolaterally directed tube-like processes. The latter do not occur in *C. rigidus* on the thecae immediately following the hooked ones. Thus the suggested origin of *M. marri* is depicted in Fig. 22 where it will be noted, additionally, that there are no stratigraphical problems with which to contend. Following the split giving rise to the *priodon*-line both *Monograptus* s.s. and *Monoclimacis* expanded into numerous species. *M. marri* extends up to the *crispus* and possibly *griestoniensis* Zones where it becomes difficult to distinguish the two species *M. marri* and *M. priodon*. It seems certain that the latter evolved from *M. marri* by the formation of a longer thecal hook with an entire dorsal lip, and by increased robustness of the rhabdosome as a whole. Whilst more slender forms were evolved at times (e.g. *M. parapriodon* Bouček) the essential evolution was to the Wenlock robust forms of *M. priodon* and later to the robust and spinose *M. flemingii*. Offshoots from the main line almost certainly produced various species such as *M. firmus* Bouček, *M. radotinensis* Bouček, *M. riccartonensis* Lapworth etc. each of which has various biocharacters developed at the expense of others. Various collections of *M. riccartonensis* show that extreme variants have pronounced dorsal flexure, in contrast to the usual gentle flexure, and it is almost certain that there is a progression through *M. flexilis belophorus* to *M. flexilis flexilis* in which the dorsal curvature is both pronounced and characteristic. The suggested lineage involves an increase in the metathecal proportions from the beak-like hook of *M. riccartonensis*.

One difficult problem in this interpretation has been the recent recognition of extremely robust spinose *priodon*-types in the *turriculatus* Zone. Bassett &

Rickards (1971) described *Monograptus* sp. A from the *turriculatus* Zone of Cross Fell, northern England, the Southern Uplands and from Norway. This was later described by Hutt (1975), with additional evidence from the Lake District (Fig. 22). The species bears a striking resemblance to the middle and upper Wenlock *M. flemingii* (Salter) and can only be interpreted, whatever its origin, as having achieved the *flemingii* condition at an extremely early stage in the evolution of the group. In this respect it parallels the lobate *M.* sp. B from the *magnus* Zone, and as has been suggested earlier in this account, innovation often seems to occur firstly with great rapidity to be followed by a less successful (morphologically speaking) attempt to achieve the same thing. The rapid innovation is, in effect, 'before its time' and usually characterizes a short side line of evolution. *M.* sp. A of Bassett & Rickards almost certainly belongs in this category.

Mediograptus Bouček & Přibyl (*in* Přibyl 1948) is said to differ from *Globosograptus* and *Streptograptus* by the 'less coiled ends of the thecae'. *Streptograptus* is discussed below (p. 67), but it has been shown that some forms usually placed in *Streptograptus* (*M. antennularius* Meneghini) have exactly the same thecal hooks as others placed in *Mediograptus* (*M. minimus cautleyensis* Rickards ; Bulman & Rickards *in* Bulman 1970 ; Fig. 28). In both these species the dorsal and ventral walls participate in what is virtually a *priodon*-type hook except that the ventrolateral processes typical of the latter are reduced to rather rounded wing-like processes. It is certain that other *Mediograptus* and *Streptograptus* species have the same structure, that the thecae are not 'coiled' in any way, and that they are best regarded

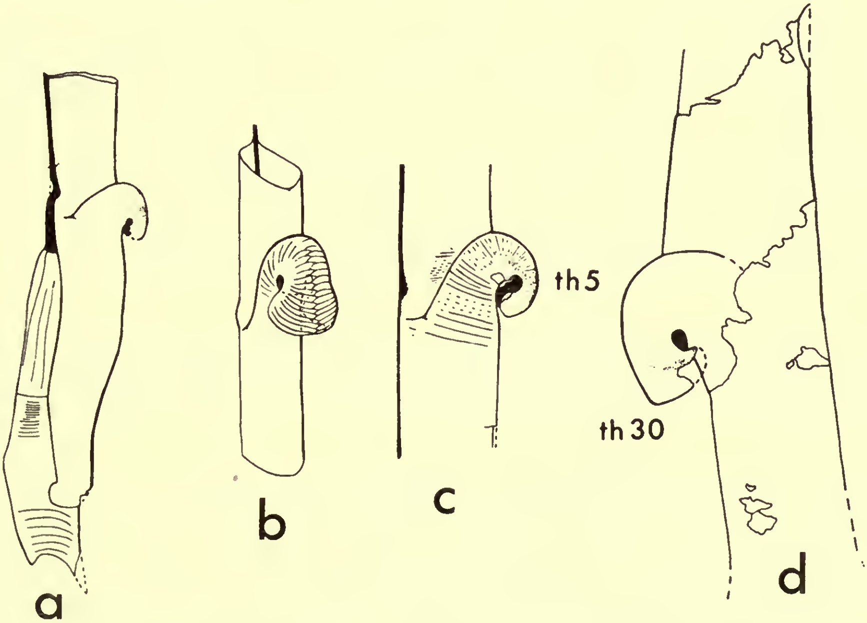


FIG. 28. a–c, '*Mediograptus*' *minimus cautleyensis* ; d, '*Streptograptus*' *antennularius* ; after Bulman & Rickards (*in* Bulman 1970). ×50.

as *Monograptus sensu stricto* which have evolved from either the main *priodon* lineage or the *lobiferus* lineage by acquiring slight rhabdosomal changes (Fig. 29). The rhabdosomes may be almost straight, dorsally or ventrally curved, or both. As in other groups with more slender species (e.g. *Oktavites*, p. 73) rhabdosomal curvature seems of little classificatory value.

The structure of *Globosograptus* species is less certain, but the distal thecae, whilst still axially elongated in the manner of the proximal ones, are higher with a supposed 'enrolled' late metathecal portion. The nature of the hook has not yet been determined and the affinity of the few species sometimes placed here, as well as the value of the 'genus' itself, is very doubtful.

Another problematical morphological feature of some *Monograptus* species is the recently-discovered prothecal fold. Prothecal folds have been discerned in some species previously regarded as mediograptids but which are here considered somewhat simplified offshoots from *Monograptus* (Fig. 29); they are also known in *Oktavites* (p. 73) and in streptograptids (Figs 29, 32) and, again, may reflect a trend affecting several different lineages at more or less the same time, namely from near the base of the *turriculatus* Zone upwards.

From the above it will be clear that we consider *Monograptus sensu stricto* to be polyphyletic. Whilst there may be some clarity around the *priodon*, *undulatus* and *lobiferus* lineages this does not extend to include evolution within '*Mediograptus*', '*Globosograptus*' and '*Streptograptus*'. The last occurrences of *Monograptus sensu stricto* are in the low Ludlow in the form of such species as *M. unguiferus* Perner and *M. uncinatus* Tullberg. One of us (R. B. R.) has isolated specimens of *M. unguiferus* (SM A64520–4) in beds yielding *M. colonus compactus* Wood and *P. dubius* (Suess), and these, like Urbanek's (1958) specimens of *M. uncinatus*, are striking in their resemblance to low Wenlock specimens of *M. priodon*. Unlike the late Ludlow and early Devonian hooked monograptids, *M. unguiferus* and *M. uncinatus* are undoubtedly related to the earlier *priodon–flemingii* lineage although the poor record of them in the *ludensis* Zone remains a problem (see section II above, p. 10). Nevertheless this relatively small gap in the record hardly compares with that between the *nilssoni–scanicus* Zones and the *fecundus* Zone where links between the *priodon* and *hercynicus* lines are lacking.

35. *Pristiograptus*. Reference to Fig. 1 (p. 7) will indicate the highly important nature of this genus in the evolution of the Silurian graptolites: from it stems the last known evolutionary burst of graptoloids. Like *Monoclimacis* the early evolution

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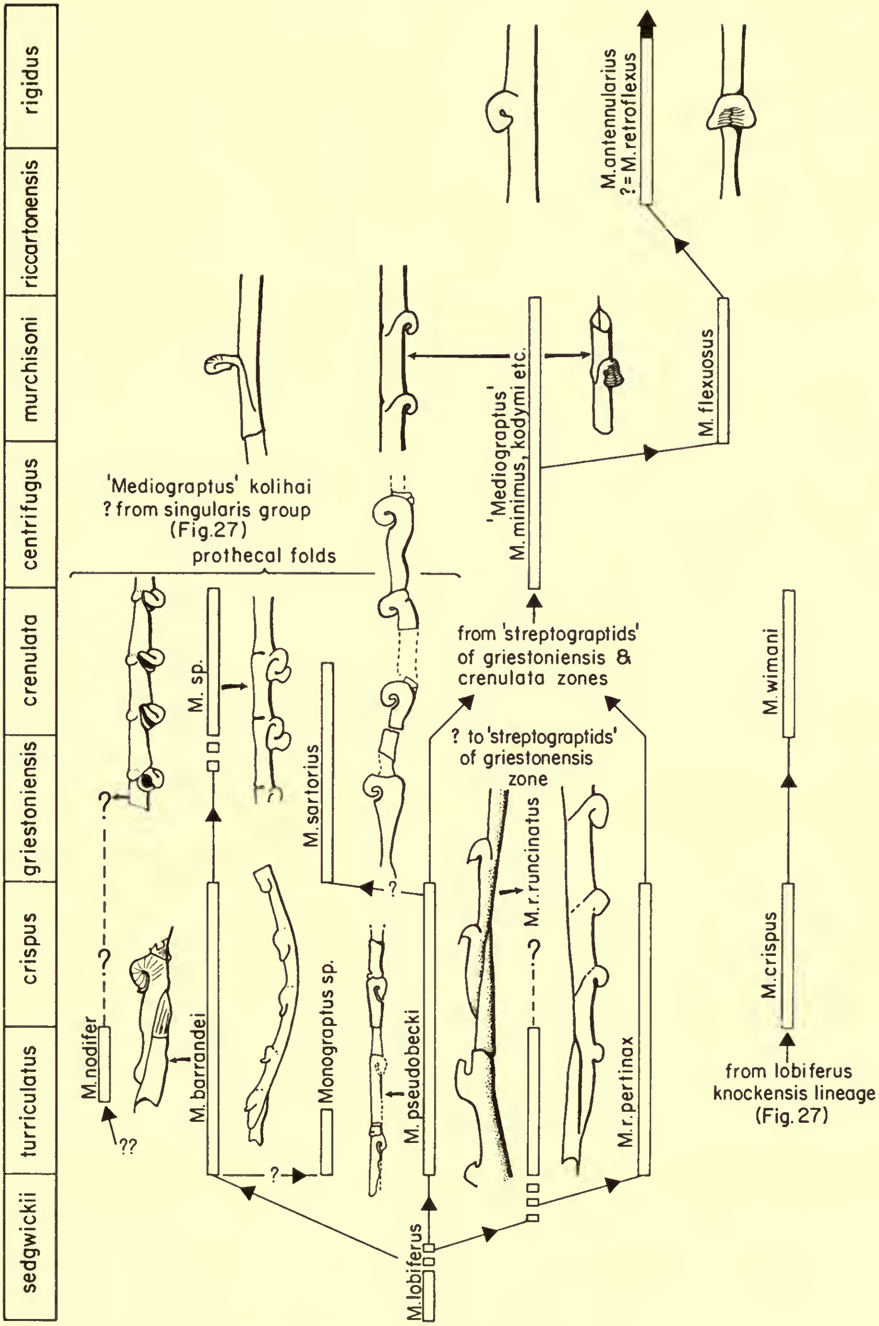
Fig. 29. Evolution of '*Streptograptus*', '*Mediograptus*' and other lobate monograptids: *M. pseudobecki*, TCD 8638, × 11¼; *M. r. runcinatus*, Lapworth Collection, after Strachan (1952), × 11¼; *M. r. pertinax*, LU 57728, × 11¼; *Monograptus* sp., LU 57715, × 11¼; *M. barrandei*, Riksmuseum Cn 54924, × 13½ approx.; *M. nodifer*, LO 1041t, × 9 approx.; *Monograptus* sp. showing superficial resemblance to *M. nodifer* but with excessive growth of the dorsal, as opposed to ventral, margin of the thecae, × 9 approx.; *M. sartorius*, LO 1032t, × 11¼; '*Mediograptus*' *kolihai*, after Rickards & Iordan (1975), × 11¼; '*Mediograptus*' *minimus*, after Bulman & Rickards (*in* Bulman 1970), × 13½ approx.; *M. antennularius*, after Bulman & Rickards (*in* Bulman 1970), × 9 approx.


sedgwickii
turriculatus
crispus
griestoniensis
crenulata
centrifugus
murchisoni
riccartonensis
rigidus
M.lobiferus
M.nodifer
??
?
M.barrandei
M.sp.
Monograptus sp.
M.sartorius
M.pseudobecki
M.r.runcinatus
M.r.pertinax
? to 'streptograptids' of griestonensis zone
from 'streptograptids' of griestoniensis & crenulata zones
'Mediograptus' kolihai ? from singularis group (Fig.27)
prothecal folds
'Mediograptus' M. minimus, kodymi etc.
M.flexuosus
M.antennularius ?=M.retroflexus
M.crispus
M.wimani
from lobiferus knockensis lineage (Fig.27)

was rather slow, and its roots have previously been considered obscured in the great plexus of low to middle Llandovery evolution. The earliest robust pristiograptid of which we are aware is *P. concinnus* (Lapworth) which occurs in the *argenteus* Zone in the Howgill Fells (Rickards 1970) and Lake District, and also as low as the *triangulatus* Zone in the Lake District and Rheidol Gorge. The species is very close to *A. atavus*, retaining a slight geniculation reflected mainly in the gently convex free ventral wall, and in fact is morphologically and stratigraphically intermediate between *A. atavus* and *P. regularis* (Fig. 30; Pl. 5, fig. 7). The last species has lost all traces of the geniculum but retains the long slender rhabdosome of the earlier forms and the relatively small early thecae and sicula. The lineage also exhibits a gradual reduction in the length of the sicula compared with its *atavus* ancestors.

The only other early *Pristiograptus* species are *M. fragilis fragilis* Rickards (*cyphus–convolutus* Zones), *M. f.* subsp. Hutt (*acinaces* and *cyphus* Zones) and two undescribed forms from the *magnus* Zone of the Lake District (Figs 30, 55). *P. fragilis* probably reflects a tendency to gracilization on the part of the *A. atavus* stock: geniculation had already been lost and the thecae are long, quite simple tubes. Once again these forms are best regarded as an early successful production of the pristiograptid morphology, to be followed by a slower, less spectacular repeat of the same process in the *atavus–concinnus–regularis* lines. The two undescribed forms (Figs 55a, b) are clearly of this latter lineage, and may actually be morphological intermediates between *P. concinnus* and *P. regularis*, just as they are stratigraphical intermediates.

Thus the *regularis* line was established quite low in the Llandovery. It persists into the basal Wenlock where it is represented by one species (*P. watneyae* Rickards). In order of appearance in the record the *regularis* line is represented by the following species:

1. *P. concinnus* (*triangulatus–sedgwickii* Zones)
2. *P. jaculum* (*argenteus–sedgwickii* Zones)
3. *P. regularis* (*convolutus–turriculatus* Zones)
4. *P. variabilis* (*turriculatus–crispus* Zones)
5. *P. nudus* (*turriculatus–crenulata* Zones)
6. *P. watneyae* (*centrifugus* Zone)

All these species, and their subspecies, have very long rhabdosomes, occasionally up to 200 mm, and slender, straight proximal regions with small siculae. *P. nudus* (Lapworth) (Pl. 2, fig. 5) is the first species to deviate from the group pattern in that the proximal end is rather more robust and occasionally with slight ventral curvature

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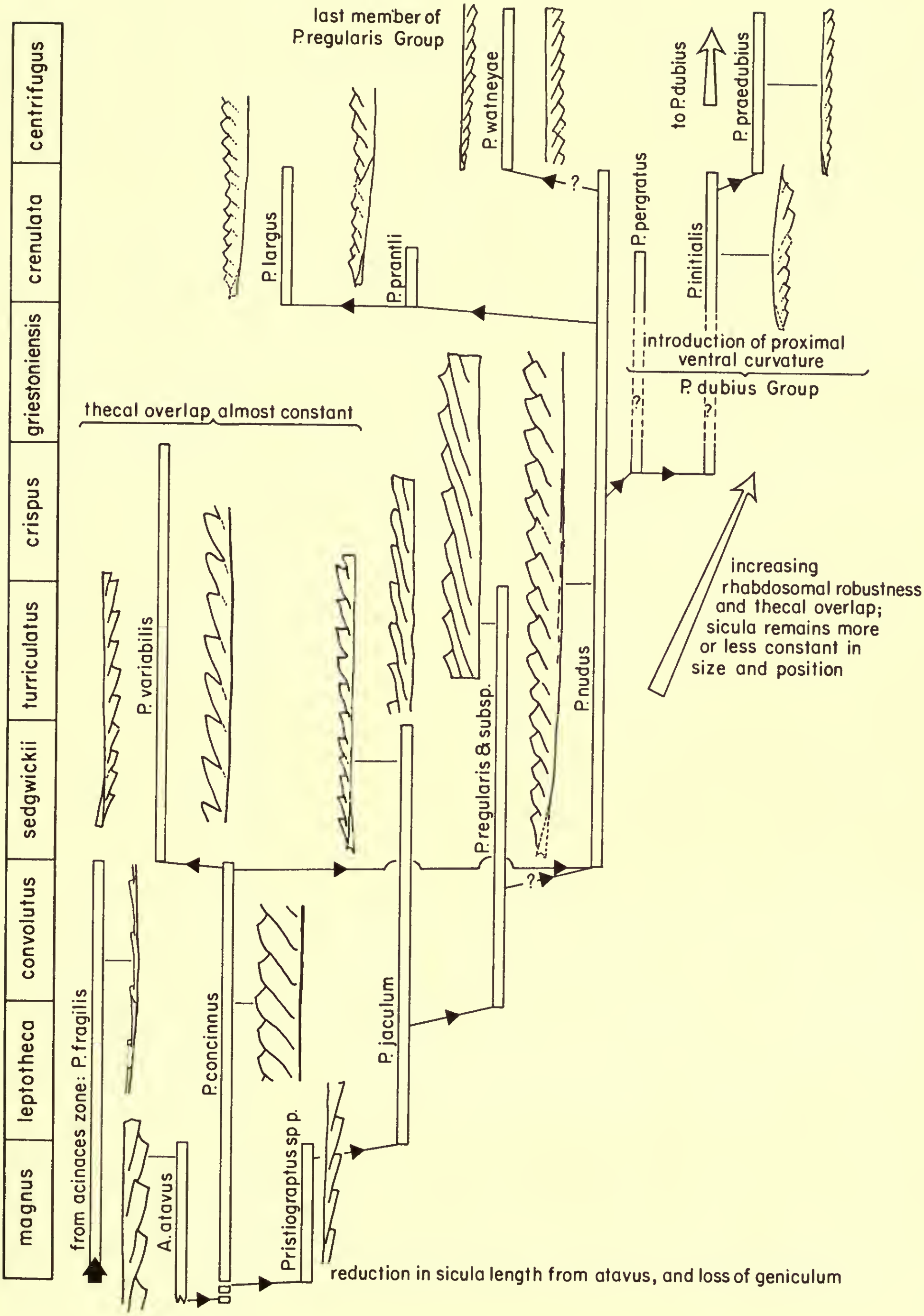
FIG. 30. Evolution of the Llandovery *Pristiograptus* species: *P. fragilis*, LU 57587, ×4½; *P. concinnus*, after LU 57564, ×4½; *P.* sp. after LU 57772, ×4½; *P. jaculum*, after Elles & Wood (1901–18: text-fig. 244a) and BU 1459, ×4½; *P. variabilis*, SM A21634 and SM A21635, ×4½; *P. regularis*, SM A20956, ×4½; *P. nudus*, HUR 5Wi/6, ×4½; *P. largus*, after Přibyl (1945), ×2¼; *P. prantli*, after Přibyl (1945), ×2¼; *P. watneyae*, HUR 37W/17, ×2¼; *P. initialis*, after Přibyl (1945), ×2¼; *P. initialis*, after Přibyl (1945), ×2¼; *P.* cf. *praedubius*, SM A52621, ×2¼.


magnus
leptotheca
convolutus
sedgwickii
turriculatus
crispus
griestoniensis
crenulata
centrifugus
from acinaces zone: P. fragilis
A. atavus
P. concinnus
Pristiograptus spp.
P. jaculum
P. variabilis
P. regularis & subsp.
P. nudus
P. largus
P. prantli
P. watneyae
last member of P. regularis Group
P. pergratus
P. initialis
P. praedubius
to P. dubius
?
thecal overlap almost constant
introduction of proximal ventral curvature
P. dubius Group
increasing rhabdosomal robustness and thecal overlap; sicula remains more or less constant in size and position
reduction in sicula length from atavus, and loss of geniculum

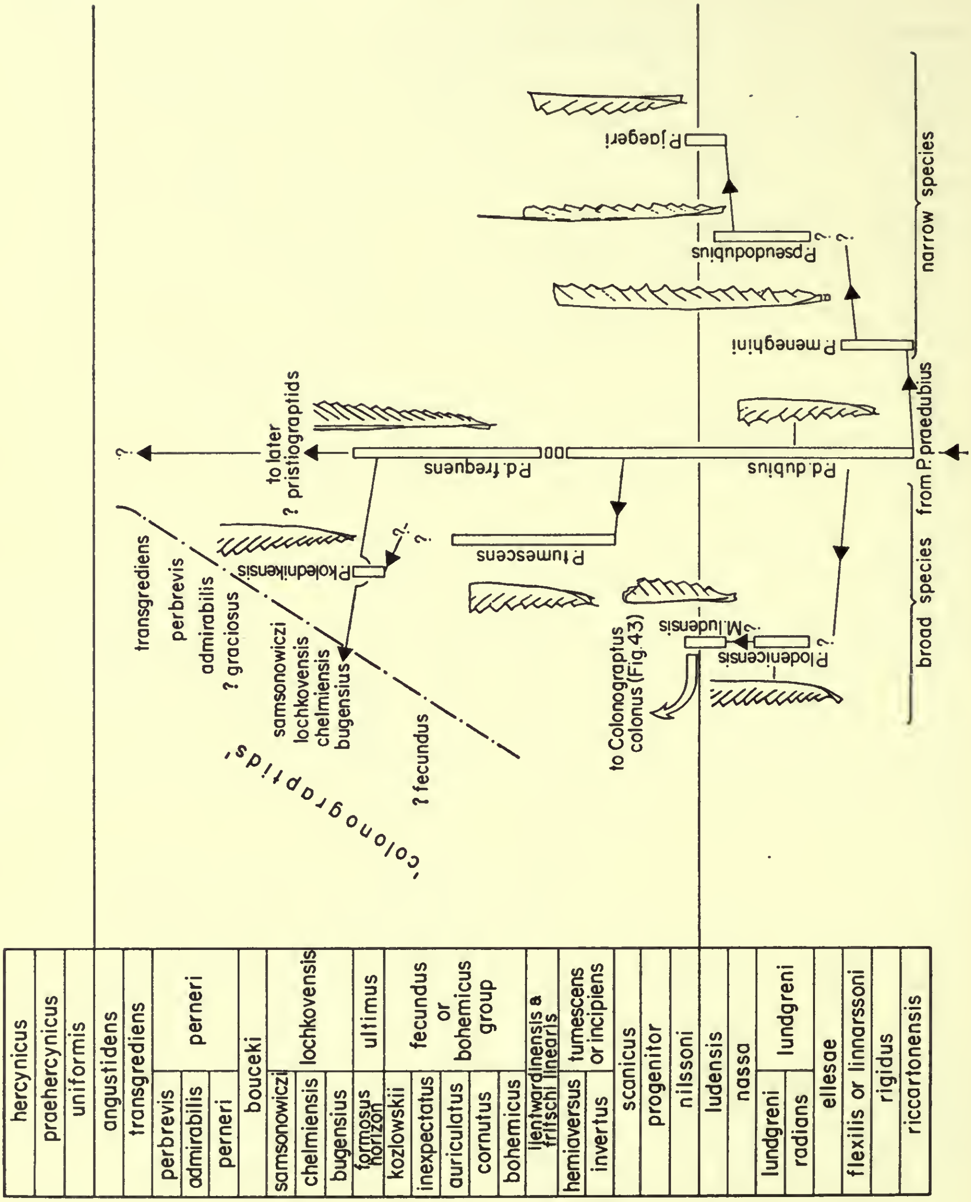

P. jaegeri
P. pseudodubius
P. meneghini
narrow species
broad species
from P. praedubius
Pd. dubius
Pd. frequens
to later ? pristiograptids
P. tumescens
P. kolednikensis
M. ludensis
P. lodenicensis
to Colonograptus colonus (Fig. 43)
transgrediens
perbrevis
admirabilis
? graciosus
samsonowiczi
lochkovensis
chelmiensis
bugensius
? fecundus
'colonograptids'
hercynicus
praehercynicus
uniformis
angustidens
transgrediens
perneri
perbrevis
admirabilis
perneri
bouceki
lochkovensis
samsonowiczi
chelmiensis
bugensius
ultimus
formosus horizon
fecundus or bohemicus group
kozlowskii
inexpectatus
auriculatus
cornutus
bohemicus
lientwardinensis & fritschi linearis
tumescens or incipiens
hemiaversus
invertus
scanicus
progenitor
nilssoni
ludensis
nassa
lundgreni
lundgreni
radians
ellesae
flexilis or linnarssoni
rigidus
riccartonensis

FIG. 31. Evolution of Wenlock and later *Pristiograptus* species: *P. dubius*, BU 1463; *P. meneghini*, HUR 17N/46; *P. pseudodubius*, HUR 26N/11; *P. jaegeri*, TCD 8661; *P. lodenicensis*, after Přibyl (1945); *'Monograptus' ludensis*, SM A60900; *P. tumescens*, BU 1472; *P. dubius frequens*, after Přibyl (1945); *P. kolednicensis*, after Přibyl (1945). All figures ×2½.

(Fig. 30). *P. denemarkae, P. pergratus* and *P. initialis* (*crenulata* Zone) almost certainly evolved from *P. nudus* (Fig. 30) and this line led to the low Wenlock *P. praedubius* and hence to the critically important *P. dubius* lineage which then persisted into the Pridoli. The *regularis* lineage is essentially Llandovery, and the *dubius* lineage essentially Wenlock upwards, but the two overlap briefly in the *crenulata* to *centrifugus* Zones.

Through the Wenlock *P. dubius* repeatedly produced short-lived broad and narrow species and subspecies: *P. dubius latus* Bouček, *P. pseudolatus* Rickards, *P. meneghini* (Gortani) and *P. pseudodubius* (Bouček). The tendency was continued less spectacularly in the Ludlow (e.g. *P. d. ludlowensis* Bouček, *P. frequens* Jaekel and *P. vicinus* Perner), but more importantly the *P. dubius* lineage provided the basic stock for many genera by spectacular modifications of the simple, tubular, pristiograptid aperture (*Colonograptus* etc.). These modifications are dealt with in the appropriate sections below (42 onwards, pp. 77–82).

36. '*Streptograptus*'. A large number of species were placed in Yin's (1937) genus by Bouček & Přibyl (1943) but the type species, *M. nodifer* Törnquist, is at present unique in its thecal structure (Fig. 32). Other species commonly placed

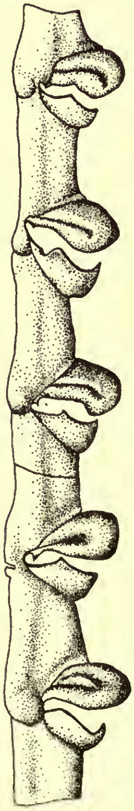


FIG. 32. *Monograptus nodifer* Törnquist, LO 1041t, ×20, showing the unique thecae of the type species of '*Streptograptus*'; the ventral flange may be formed by excessive growth of the ventral thecal wall; probably *turriculatus* Zone.

here (*M. antennularius*, *M. exiguus* Nicholson) we include in other genera on the evidence provided by detailed morphological studies (pp. 63, 73). But the structure of a majority of the species included in *Streptograptus* by Bouček & Přibyl is unknown, although it can be confidently predicted that some will turn out to have the *Monograptus* s.s. thecae of *M. antennularius*: if and when this is established it may be possible to elucidate the evolution of the *antennularius* types.

Hutt *et al.* (1970) described a species as *M.* cf. *barrandei sensu* Elles & Wood in which the thecae exhibit prothecal folds and a strongly retroverted or lobed dorsal thecal wall with little or no growth of the ventral thecal wall (Fig. 29). The apertural region of the dorsal wall has an upturned median lip. The horizon is low in the *turriculatus* Zone of Dalarne, Sweden. It is possible that this thecal type is ancestral to the more complex *nodifer* type which is typical of higher horizons (? *turriculatus* to *crenulata* Zones). *M.* sp. Hutt (*turriculatus* Zone) is a possible intermediate in that it has attained the *nodifer* fish-hook rhabdosome but still has the *barrandei* hook and upturned lip. Excessive growth of this lip, to the extent that it finally resulted in the aperture facing the dorsal margin, would lead to *M. nodifer* s.s. (Fig. 29).

M. nodifer was recorded from the *turriculatus* and *crispus* Zones by Elles & Wood (1901–18) but it is far from certain from their figured specimens whether these

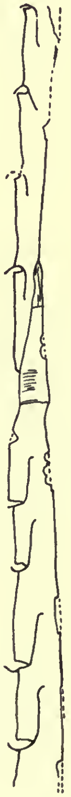


FIG. 33. *Monoclimacis* cf. *griestoniensis* (Nicol), Oslo Museum 39550, × 12½, a bipolar siculate rhabdosome; high Llandovery.

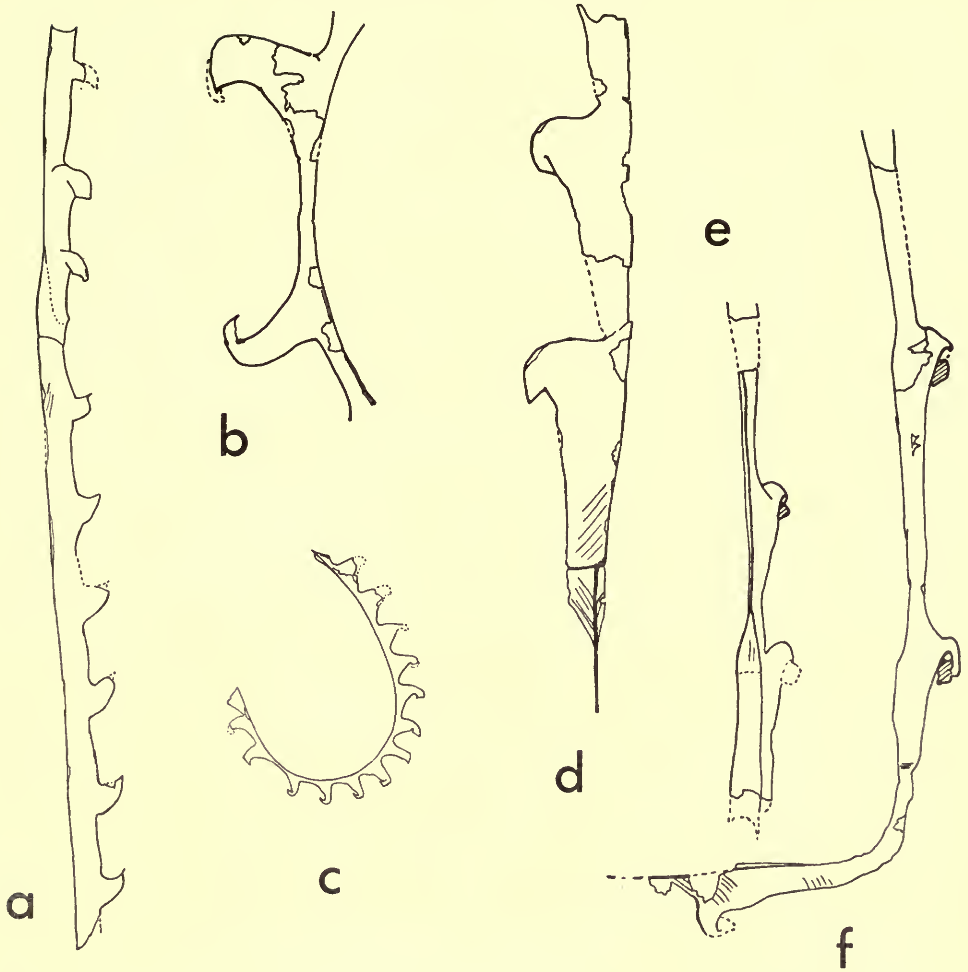


FIG. 34. Comparison of siculate bipolar rhabdosome (a) with regenerative bipolar rhabdosomes: a, *Monograptus sedgwickii*, GSM CV7645, × 12½, *sedgwickii* Zone; b, c, *M.* cf. *decipiens*, GSM NIC5076/7, × 12½ and × 2½ respectively, *convolutus* Zone; d, early regenerative growth of *M. lobiferus*, SM A81836, × 12½, *convolutus* Zone; e, f, siculate specimen and regenerative specimen of *M.* aff. *sartorius*, LO temporary no. 111, × 12½.

really are Törnquist's species. On the other hand, Hutt (1975) has recorded *M. nodifer* ? from the *turriculatus* Zone of the Lake District, so that the *nodifer* hook *may* appear as early as this zone.

Finally we would mention species such as *M. runcinatus* Lapworth, sometimes placed in *Diversograptus*, in which the hook (considered a lobe by Bouček & Přibyl 1943) seems not unlike the *undulatus* type. Some similar species, whether with prothecal folds or not, are probably best considered in *Monograptus* s.s. and not as streptograptids, the usual practice.

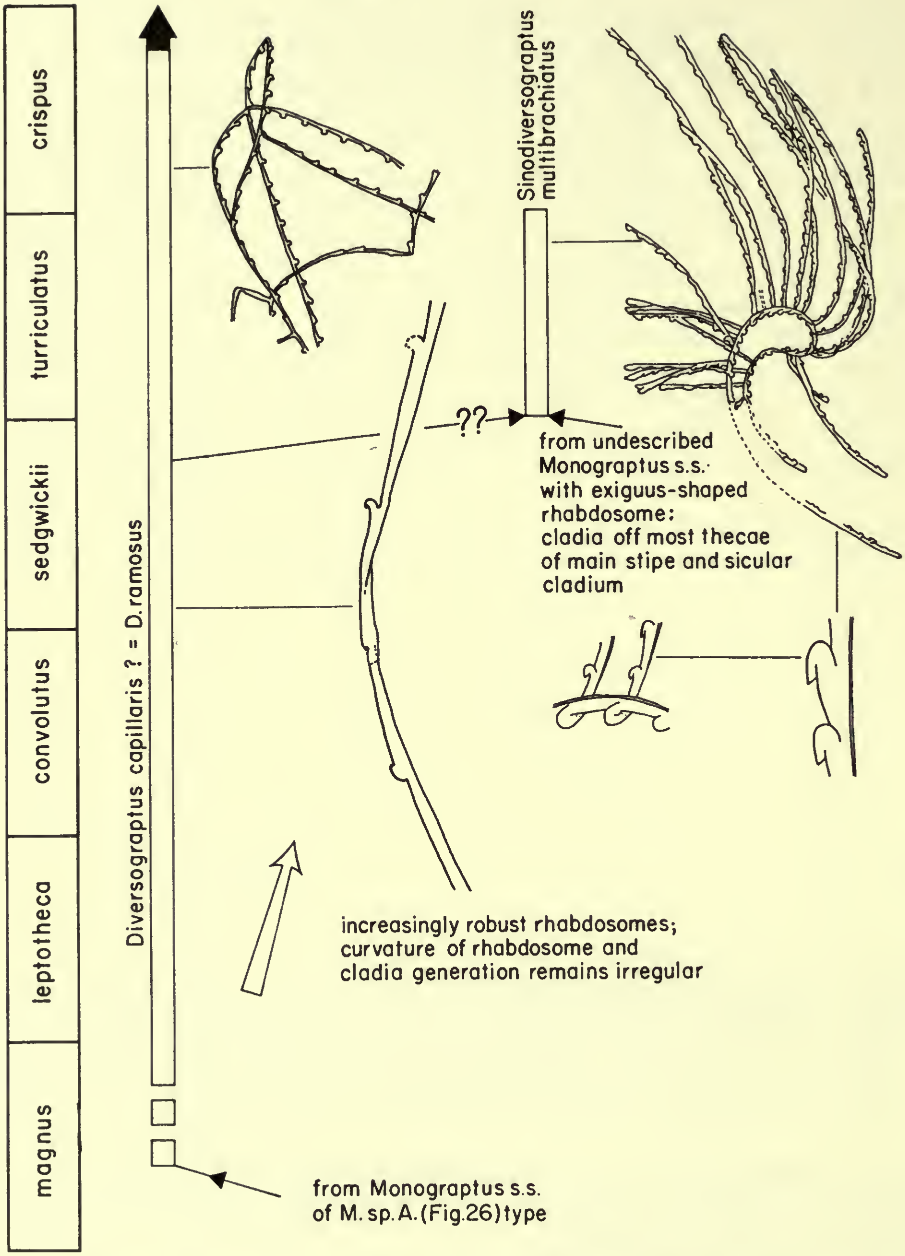

crispus
turriculatus
sedgwickii
convolutus
leptotheca
magnus
Diversograptus capillaris ? = D. ramosus
Sinodiversograptus multibrachiatus
??
from undescribed Monograptus s.s. with exiguus-shaped rhabdosome: cladia off most thecae of main stipe and sicular cladium
increasingly robust rhabdosomes; curvature of rhabdosome and cladia generation remains irregular
from Monograptus s.s. of M. sp. A. (Fig. 26) type

FIG. 35. Evolution of *Diversograptus* and *Sinodiversograptus*: *D. ramosus*, proximal end × 35 approx., Royal Institute of Natural Sciences, Belgium, IG11.077; cladia-bearing portion of rhabdosome, × 2, after Bouček & Přibyl (1954); *Sinodiversograptus multibrachiatus*, × 1½, × 5 and × 10 respectively, after Mu & Chen (1962); specimen no. 11580a.

37. *Diversograptus, Sinodiversograptus* and *Barrandeograptus*. The genus *Diversograptus* Manck has recently been revised by Rickards (1973) who demonstrated that sicular cladia were present on the type specimens, and were also found in quite unrelated groups, such as in *Monoclimacis* cf. *griestoniensis* Nicol (Fig. 33). The diversiform procladium condition, as opposed to bipolar rhabdosomes resulting from regeneration of broken stipes (Fig. 34), is a late astogenetic growth stage potentially achievable in most monograptid groups although it has not yet been established in any members of the *priodon* lineage. Regeneration of broken stipes is similarly to be found in a number of groups including triangulate monograptids (Fig. 34) and is no criterion for inclusion in the genus *Diversograptus*.

Diversograptus and *Sinodiversograptus* are probably of some value as genera at present since both the main stipe and sicular cladium generate at least secondary cladia. In *Diversograptus* these are widely spaced and irregular in distribution, even uncommon, but in *Sinodiversograptus* they are developed from most of the main stipe thecae and sicular cladial thecae. The hooks in both genera are of the *undulatus* or *lobiferus* type, that is *not* enrolled tightly, and it is certain that they evolved from *Monograptus* s.s. not from *Streptograptus* as commonly supposed. One of us (R. B. R.) has been fortunate enough to examine good specimens of *Sinodiversograptus* from Tienshan, and, like the figures of the Chinese specimens, these exhibit an *undulatus* type of hook (Fig. 35). The main stipe is of *exiguus*-

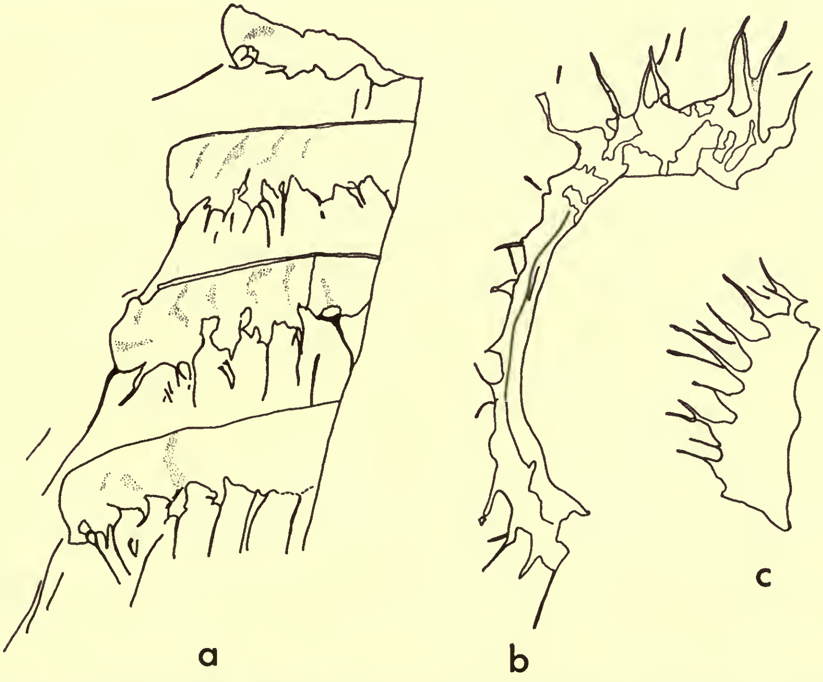


FIG. 36. a–c, *Monograptus turriculatus* (Barrande), specimens suggesting complicated spinose apertural processes; respectively GSM RS6614, LU 57699, LU 57695; *turriculatus* Zone, Cross Fell (a) and Pull Beck, Lake District; all figures × 12½.

like shape, it is true, but there is in the Russian *turriculatus* Zone faunas a species like *M. exiguus* in rhabdosome shape but with *undulatus* thecae. Such a species would have made a perfect ancestor for *Sinodiversograptus*.

Diversograptus probably originates in the *magnus* to *argenteus* Zones through one of the early *Monograptus* s.s. species discussed above, p. 58. Certainly the Manck type collection has specimens ranging from about this level up to the *crenulata* Zone. Very few species are involved in the opinion of Rickards (1973) who broadly divided them into *D. capillaris* (Carruthers) below and *D. ramosus* Manck at the top of the sequence. The evolution of *Diversograptus* from *Monograptus* s.s. required a degree of gracilization as well as cladia production. The fact that thecal cladia are produced suggests that its ancestor would probably have exhibited a *lobiferus*-type hook with its ventrolaterally directed processes, and was not likely to have been *M. undulatus*, which apparently lacks such processes.

Barrandeograptus Bouček (1933) is included here as a Llandovery cladia-producing genus with few species. Its nature is very poorly known. If the apertures are really introverted as indicated by Bouček & Přibyl (1952) it is possible that *B. pulchellus* (Tullberg) evolved from a species of *Pribylograptus*, although there is a considerable time lag between the two genera (Fig. 1).

38. *'Spirograptus'*. None of the species normally included in *Spirograptus* (e.g. Přibyl 1945) are known in any detail. *M. turriculatus*, the type species, has a spirally coiled rhabdosome (Fig. 36) with 'hooked' thecae and thecal spines (? more than two to each theca); other species included by Přibyl only have variable coiling and 'hooked' thecae as unifying characters. As a genus it is valueless, serving only to indicate that from the *turriculatus* Zone upwards in the Llandovery a lot of monograptid (*sensu lato*) species became variously coiled. Not surprisingly the evolution of included forms is unknown and will require a great deal of work on the thecal morphology. Some 'typical' *Spirograptus* species (e.g. *S. tullbergi*)

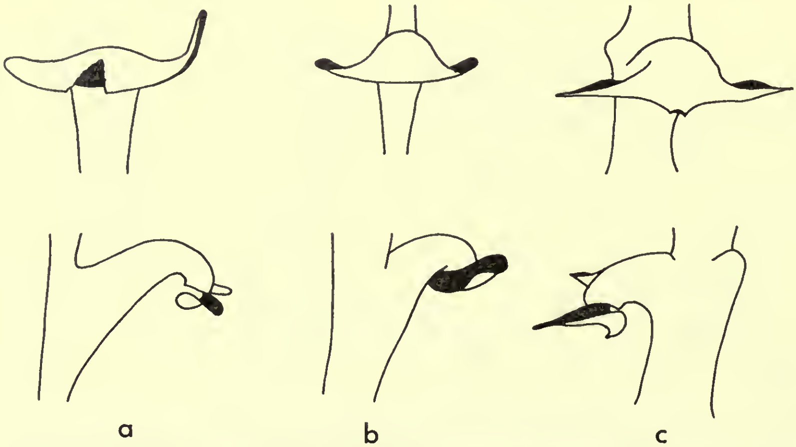


Fig. 37. Idealized sketches depicting similarity of thecal structure in *Monograptus spiralis* (*a*), *M. formosus* (b) and *M. exiguus* (c): these have respectively been referred to the genera *Oktavites*, *Monograptus* s.s. and *Streptograptus*. All figures × 20 approx.

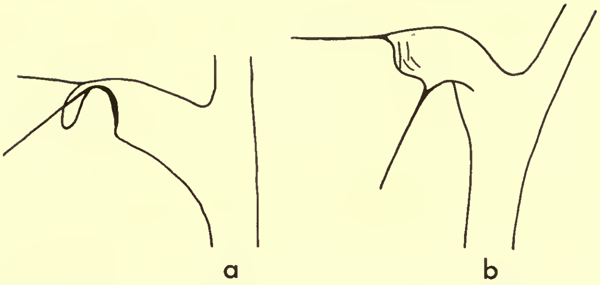


FIG. 38. Thecal structure of *M. delicatulus* Elles & Wood taken from isolated Russian specimens, courtesy of Alexandre Obut; × 25.

could readily be included on present evidence in *Campograptus, Oktavites, Spirograptus* or *Monograptus* s.s.

39. *Oktavites.* As far as we are concerned, Levina's (1928) genus includes only the type species *M. spiralis* and probably *M. exiguus* (Pl. 2, fig. 6), which although having a ventrally curved, fish-hook rhabdosome, has thecae very similar indeed to those of *M. spiralis* (Fig. 37). It is probable that some of the species at present placed in *Spirograptus* by some Continental workers actually belong here with *M. spiralis.* As with spirograptids the evolution is unknown at present, but Sudbury (1958) has suggested that *M. spiralis* evolved from the triangulate monograptid *M. delicatulus.* Although we agree with her this is in the right region of the plexus, isolated specimens of *delicatulus* (Fig. 38) suggest that the spines are too highly developed for it to be the actual ancestor of *M. spiralis.*

M. exiguus may have evolved similarly but has also been involved in the tendency, common from the *turriculatus* Zone upwards in the Llandovery, to produce a ventrally curved fish-hook rhabdosome. *M. spiralis,* and possibly other 'spirograptids', may have been ancestral to some *Cyrtograptus* species (p. 76).

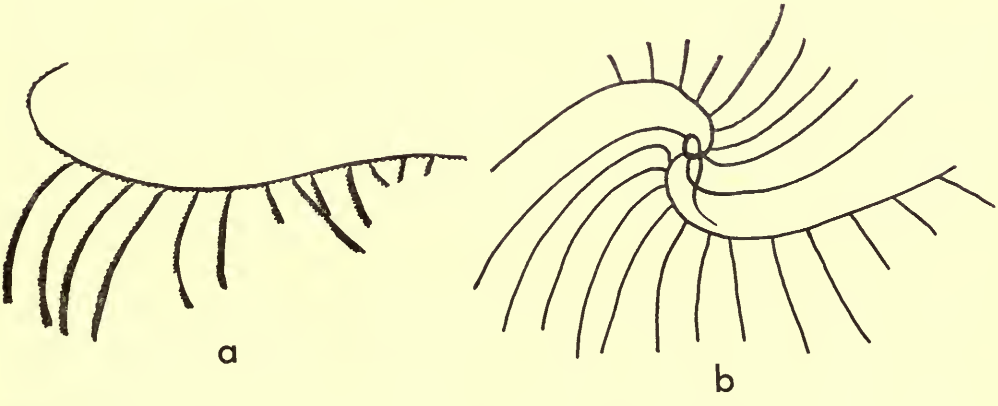


FIG. 39. a, *Uralograptus,* after Koren' (1962). b, *Averianowograptus* diagrammatic after Obut (1949) and authors' examination of original specimens, × ½.

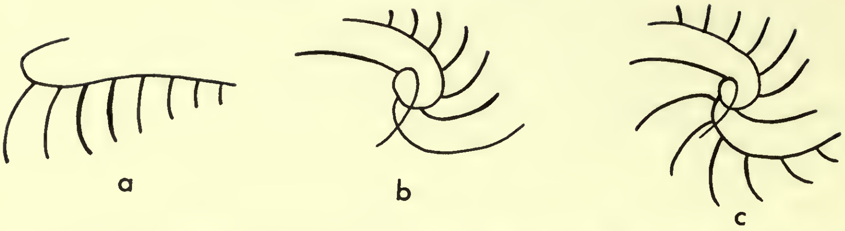


FIG. 40. Depicting manner in which *Uralograptus insuetus* (a) may have given rise to *Averianowograptus magnificus* by enrolling of the proximal end as in b, and then infilling of the gap created between the first two cladia by growth of secondary cladia on the second primary cladium (c). All figures approx. × ¼.

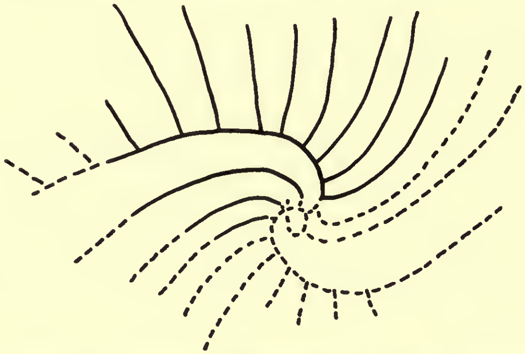


FIG. 41. Diagram depicting suggested relationship of the genus *Damosiograptus* Obut (1949), solid lines, to *Averianowograptus* Obut (1949), dotted lines *plus* solid lines ; × ½ approx.

40. *Averianowograptus* and *Uralograptus*. These two genera are typified by extremely long, slender proximal regions, hardly coiled at all, and which have axially elongate, small, slender hooked thecae. Whilst the main stipe of *U. insuetus* Koren' maintains this growth, and in the more distal regions produces numerous cladia from the hooked thecae, that in *A. magnificus* (Averianow) takes a tight coil (presumably a helical spiral) after several centimetres growth and only then produces cladia (Fig. 39). This, and the fact that in *A. magnificus* only the second cladium produced secondary cladia, is the main difference between this genus and the robust *Cyrtograptus* species such as *C. centrifugus* (p. 76).

As a purely speculative suggestion it is possible that *Averianowograptus* has evolved from *Uralograptus* by the latter developing a spiral coil between or about

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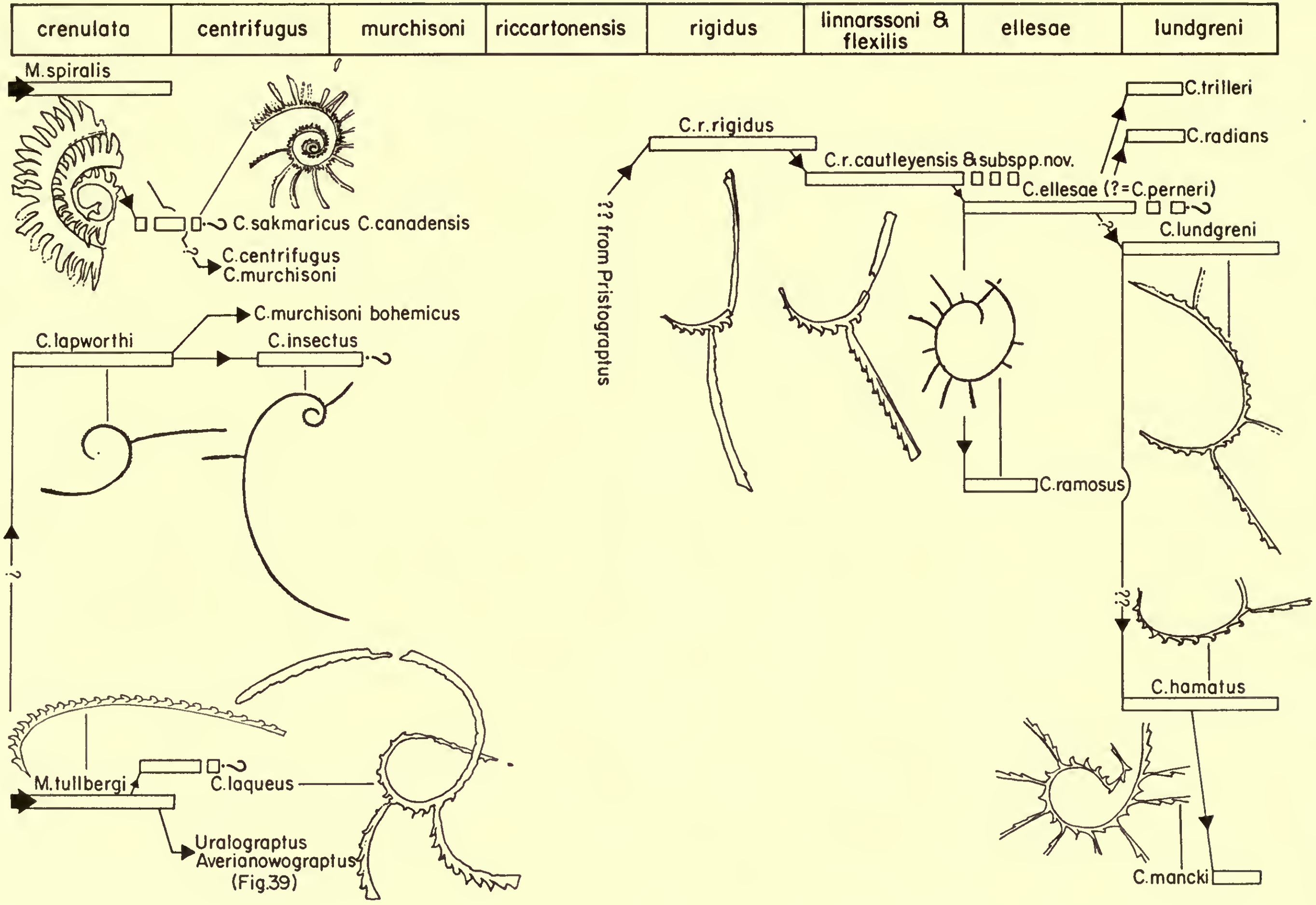
FIG. 42. Evolution of *Cyrtograptus* and related genera : *M. spiralis* after Jackson & Etherington (1969), × 2¼ ; *C. sakmaricus* after Koren' (1968), × 0·45 ; *C. lapworthi* and *C. insectus* after Bouček (1933), × 0·45 ; *M. tullbergi*, HUR S97,5.5/11, × 1¾ ; *C. laqueus* after Jackson & Etherington (1969), × 1¾ ; *C. rigidus rigidus*, SM A75341, × 1¾ ; *C. rigidus cautleyensis*, SM A55217, × 1¾ ; *C. ramosus* after Bouček, (1933), × 0·45 ; *C. lundgreni*, SM A75269, × 1¾ ; *C. hamatus*, GSM 10719, × 1¾ ; *C. mancki*, after Bouček (1933), × 1¾.


crenulata
centrifugus
murchisoni
riccartonensis
rigidus
linnarssoni & flexilis
ellesae
lundgreni
M.spiralis
C.sakmaricus C.canadensis
?
C.centrifugus
C.murchisoni
C.murchisoni bohemicus
C.lapworthi
C.insectus
?
M.tullbergi
C.laqueus
?
Uralograptus
Averianowograptus
(Fig.39)
C.r.rigidus
?? from Pristograptus
C.r.cautleyensis & subspp.nov.
C.ellesae (?=C.perneri)
?
C.lundgreni
C.trilleri
C.radians
C.ramosus
??
C.hamatus
C.mancki

the position of its first and second cladia : such a change would open a gap between those cladia which could be filled by secondary cladia off the second primary cladium (Fig. 40). *Damosiograptus* Obut (1949), the type specimen of which has been examined by one of us (R. B. R.), is a junior synonym of *Averianowograptus* (Fig. 41). It is possible that *Averianowograptus* has been somewhat superfluously split off from *Cyrtograptus* for there are some undoubted *Cyrtograptus* species which have relatively open proximal coils (*C. insectus* Bouček, *C. lapworthi* Tullberg).

41. *Cyrtograptus.* The oldest cyrtograptids, those of the latest Llandovery and earliest Wenlock, appear to include at least three main lineages, all of which may have developed from the *spiralis* complex. *M. spiralis* itself occurs in abundance in late Llandovery age rocks in many parts of the world (see Jackson & Lenz 1962, Obut, Sobolevskaya & Bondarev 1965, Obut & Sobolevskaya 1966, Jackson & Etherington 1969, Teller 1969, Berry & Murphy 1974) and exhibits some morphological variation, from one locality to another, in tightness of coiling and at least the apparent degree to which the thecae are hooked. When flattened specimens of *spiralis* have been compared closely with the proximal parts of highly coiled late Llandovery cyrtograptids such as *C. sakmaricus* Koren' (Berry & Murphy 1974) little difference between them may be noted. Indeed, the similarities suggest that a local population of *M. spiralis* was probably ancestral to that stock of late Llandovery and early Wenlock cyrtograptids which have highly and relatively tightly coiled proximal regions (*C. sakmaricus* Koren', *C. canadensis* Jackson & Etherington, *C. coroniformis* Golikov, *C. shishkaticus* Golikov, *C. centrifugus* Bouček, and possibly *C. murchisoni* Carruthers).

A second stock of latest Llandovery–earliest Wenlock cyrtograptids is exemplified by *C. lapworthi,* which has a relatively openly coiled proximal region and a single cladium that commonly develops from a theca on the most highly curved part of the main stipe. The main stipe commonly widens relatively rapidly. Specimens of *C. lapworthi,* the oldest member of the stock, are widely found and commonly numerous. They exhibit a relatively high degree of morphologic variation in rate of widening and degree to which the thecae are hooked in the proximal part of the rhabdosome. Some specimens appear similar to *M. planus.* The *C. lapworthi* lineage may have developed from *planus* or a *planus*-like form.

The third stock that appears to be present among the latest Llandovery–earliest Wenlock cyrtograptids is exemplified by *C. laqueus* Jackson & Etherington and *C. parvulus* Golikov. These have a relatively open coil and relatively few (commonly two to five) cladia. Proximal ends are characteristic, being straight and relatively thin and widening relatively slowly. The stock could have developed from *M. tullbergi* or a similarly openly-curved 'spirograptid'.

After a modest initial burst in stocks and number of species in the latest Llandovery–earliest Wenlock interval, cyrtograptids appear to have declined remarkably. No species has been recorded from the *riccartonensis* Zone, at least in those parts of the world in which it may be recognized. Coeval strata in the Urals and western North America (Yukon, Nevada) bear somewhat different graptolite associations than in Europe (Jackson & Etherington 1969, Berry & Murphy 1974).

Strata in western North America and the Urals that *may* be coeval with the essentially European *riccartonensis* Zone do bear a few cyrtograptids, which appear to be of the *C. lapworthi* type.

The marked reduction among cyrtograptids at about the interval of the *riccartonensis* Zone of the early Wenlock is followed by appearance of the *C. rigidus* lineage the origin of which is in doubt (Fig. 42). The earliest forms in this lineage (*C. r. rigidus*) may have the cladium developed from th4. Cladial development is delayed to later thecae in stratigraphically higher members of the lineage. A possible ancestral species may have been lacking in cladia and possibly even thecal hooks. Trends in the *C. rigidus* line include both delay of the cladium and gracilization of the stipes (*C. perneri* and *C. hamatus*, for example). Species with many cladia and relatively tightly coiled rhabdosomes (*C. radians* Törnquist and *C. mancki* Bouček) may have developed from members in the *C. rigidus* lineage in the latter part of the Wenlock. Such coiled species with many cladia were short-lived.

The cyrtograptids appear to have been polyphyletic with at least four and possibly more basic stocks present within the currently recognized genus *Cyrtograptus*. Fig. 1 (p. 7), which shows the approximate number of species at each horizon, by itself suggests a polyphyletic origin for *Cyrtograptus*.

42. *Saetograptus* and *M. ludensis*. The pristiograptid stock outlined above (p. 67) probably gave rise through *M. ludensis* to *Colonograptus colonus* and *Saetograptus varians* and hence to *S. chimaera*. The detailed morphology of these forms has been described by Walker (1953), Urbanek (1958), Hutt (1969) and Holland *et al.* (1969). The beginning of the lineage involves the acquisition by

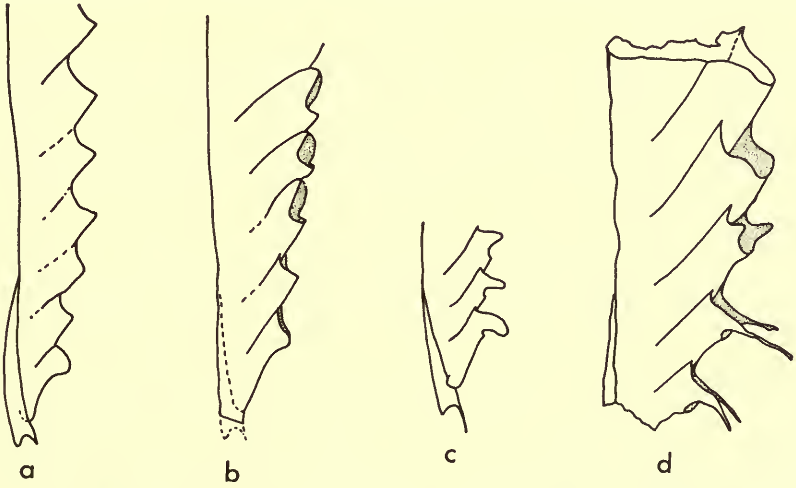


Fig. 43. a, b. '*Monograptus*' *ludensis*, respectively TCD 8658 and SM A60905 ; c, *Saetograptus* [*Colonograptus*] *colonus*, after Bulman (1970) ; d, *Saetograptus* (*Saetograptus*) *varians*, after Hutt (1969). Suggesting progressive change of paired lappets (a, b) to elongated paired lappets (c) and then to spinose, enrolled lappets (d). All figures × 12½.

M. ludensis of low paired lappets on the first and occasionally the second theca. Subsequently these became elongated in *S. colonus* and enrolled in *S. varians* and *S. chimaera* (Fig. 43). The rhabdosomes otherwise remain much the same, with distal pristiograptid thecae and slow spread of the proximal thecal type along the rhabdosome. Although it is often assumed from silhouette material that such species as *M. roemeri* Barrande and *M. leintwardinensis* Lapworth are saetograptids this has not been established from transparencies, and the work of Hutt (1969) warns of the dangers in these assumptions. More recent work by Urbanek (1970) on thecal processes in *Bohemograptus* emphasizes the point, for thecal processes need not be composed of fusellar tissue as they are in some species of *Saetograptus*. The intermediate nature of *S. varians* led Bulman & Rickards (*in* Bulman 1970) and Hutt (1969) to place *Colonograptus* Přibyl as a junior synonym of *Saetograptus* Přibyl. Saetograptids probably range into the Pridoli (*S. pilosus* Jackson & Lenz 1972 and *S. willowensis* Berry & Murphy 1974) although the detailed structure of many supposed saetograptids is not known.

43. *M. bugensius* and *M. hercynicus*. From about the level of the *ultimus* Zone upwards into the Devonian there occur a number of species which again have thecal hooks. In the case of *M. formosus* the hook is almost indistinguishable from that of the upper Llandovery species *M. spiralis* (Fig. 37, p. 72) whilst the form of the rhabdosome is close to that of some 'spirograptids' as well as to the Pridoli species such as *M. perneri* and *M. bouceki*. Others have a 'hood' from a pronounced geniculum: the hood may retreat distally so that the graptolite is biform (*M. ramstalensis* Jaeger) or it may remain throughout the length of the stipe giving an at least superficial appearance of a *Monograptus* s.s. It has been established by one of us (R. B. R.) that on specimens of *M. uniformis* from the Polar Urals this hood consists of fusellar tissue and, therefore, represents excessive growth of the dorsal thecal wall relative to that of the ventral wall.

The problem of the origin of these forms has been briefly mentioned above (p. 62), and we consider that the stratigraphic record from the *nilssoni–scanicus* Zone upwards through the Ludlow is not complete with respect to *Monograptus* s.s.; rather the late Silurian–early Devonian forms evolved independently from a pristiograptid ancestor.

The development of *Saetograptus* from *P. ludensis* by the evolution of paired lappets (Fig. 43) has already been demonstrated, and it is of interest that pristiograptids with lateral lappet structures on at least the proximal one or two thecae are present in Ludlow (*P. roemeri* Barrande) and Pridoli forms (*P. bugensis* Teller, *P. rarus* Teller and related species in the *P. transgrediens* Perner group). Dorsal coalescence of these lappet structures is all that is needed in some instances to evolve those rhabdosomes that have both hooded and pristiograptid thecae (biform rhabdosomes) and those in which all thecae are hooded. In other such rhabdosomes, a certain increase in geniculation is required (Fig. 44).

The position of the Ludlow 'monoclimacids' *M. haupti* (Kuhne) and *M. micropoma* (*sensu* Urbanek 1958) is worthy of note in regard to possible ancestors for certain late Silurian–early Devonian rhabdosomes with hooded thecal apertures on

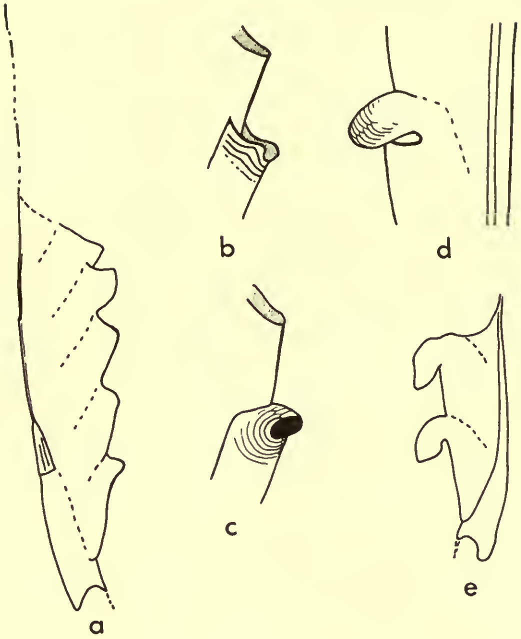


FIG. 44. Depicting the manner in which the thecal hooks or hoods of *M. uniformis* (d, e) might have developed from a paired lappet structure as exhibited by '*M.*' cf. *rarus* Teller (a, b) by dorsal coalescence of the lappets (c) ; a, '*M.*' cf. *rarus*, Romanian Geological Survey, × 12½ ; b, idealized interpretation of paired lappet structure of '*M.*' cf. *rarus* ; c, suggested dorsal coalescence of lappets to form a hook or hood ; d, sketch of fusellar structure on thecae of *M. uniformis* made by R. B. R. in the collection of Dr Koren', Leningrad, × 12½ ; e, proximal end of *M. uniformis*, after Koren' (personal communication).

some or all thecae. *M. haupti* is known to range through most if not all of the Ludlow (Teller 1969, Urbanek 1970, Jackson & Lenz 1972). Thecae in some specimens of *M. haupti* display considerable geniculation (see Urbanek 1958) as well as curvature in the proximal part of the rhabdosome similar in degree to that among certain Pridoli and younger monograptids with thecal hoods. The thecae in early Ludlow specimens of *M. haupti* as well as the range in morphological variation in specimens from several positions in the Ludlow suggest that *M. haupti* developed from a pristiograptid, possibly during the early Ludlow. Of note in this suggestion is that no post-Wenlock 'monoclimacids' are at present known with either paired lappets or other lateral processes.

Urbanek's (1958) study of the early Ludlow 'monoclimacid' *M. micropoma* indicated that the dorsal thecal flanges or genicular projections were formed from microfusellar tissue. If this were also true for *M. haupti* and some late Silurian–early Devonian monograptids with hooded or even apparently hooked thecal apertures, then the problems involved in their ancestry would be near solution.

The earliest late Silurian–early Devonian monograptid with hooded thecal apertures is *M. balticus* Teller. It occurs in late Ludlow strata (Teller 1969, Jackson & Lenz 1972). Specimens of the *angustidens–uniformis–hercynicus–yukonensis* plexus with thecal hoods strongly developed on the proximal thecae but, in some specimens, weakly developed on the distal ones appear stratigraphically low in Pridoli age beds (Jackson & Lenz 1969, Lenz & Jackson 1971, Jackson & Lenz 1972). A general trend among specimens of the *uniformis–hercynicus* group is for the distal thecae to be less strongly hooded than the proximal in relatively more specimens among the stratigraphically higher and thus younger members of this stock.

All thecae are apparently hooded in *M. balticus* and most are hooded in a majority of specimens of *angustidens* and *uniformis*. The early members of the *angustidens–uniformis* group may have developed from *M. balticus*. The first steps towards reduction in the amount of hood over the apertures in distal thecae were taken in some specimens in the *angustidens–uniformis* group.

The lineage *M. aequabilis–M. aequabilis notoaequabilis* Jaeger is characterized by the proximal one to three thecae having thecal hoods and those of the remainder of the rhabdosome being slightly to markedly geniculate. The hoods on the proximal thecae appear to be paired lateral lappets that have grown together. *M. aequabilis aequabilis* occurs in *M. uniformis* Zone beds (Jaeger 1959, Berry & Murphy 1974) in Europe and western North America (Berry & Murphy 1974). Its ancestry is uncertain, although it may have developed from a *P. transgrediens* group form.

M. hemiodon Jaeger is another early Devonian monograptid with uncertain ancestry. It has hooded proximal and strongly geniculate distal thecae. Both the *aequabilis* and *hemiodon* stocks might have developed from a *haupti*-like form in which the proximal thecae had developed paired lateral lappets that subsequently fused. No record of such a form exists, however, and the Pridoli interval separates the youngest *haupti* and the oldest specimens of the *aequabilis* and *hemiodon* stocks. Alternatively some member of the pristiograptid lineage, particularly one of the *P. transgrediens* group, or a Pridoli pristiograptid such as *P. kosoviensis* in which thecae in some specimens appear somewhat geniculate, may have been the ancestor.

M. microdon Richter is another latest Silurian–early Devonian form with unknown ancestry. *M. microdon* appears to have hooded thecae and a thin rhabdosome. Its thecae have hoods of approximately the same size throughout. It may have developed as an offshoot from the *angustidens–uniformis* stock early in the history of that group when thin rhabdosomes were common.

The youngest monograptids, those in the *yukonensis* group, appear to have come from the *angustidens–uniformis–hercynicus* group. A surprising degree of morphological variation has been described among members of the *yukonensis* group (Jaeger *in* Churkin *et al.* 1970, Jaeger *et al.* 1970, Lenz & Jackson 1971). The *yukonensis* group appears to be related to and derived from the *angustidens–uniformis–hercynicus* group through either *M. thomasi* Jaeger or *M. falcarius* Koren', or both (Koren' 1971). Stratigraphically, the former species lies above the highest *M. hercynicus* and below as well as with the lowest *M. yukonensis* (Berry & Murphy 1972). Koren' (1971) illustrated a number of rhabdosomes of *M. falcarius* that had shapes intermediate between those of the *M. hercynicus* and *M. yukonensis* group forms.

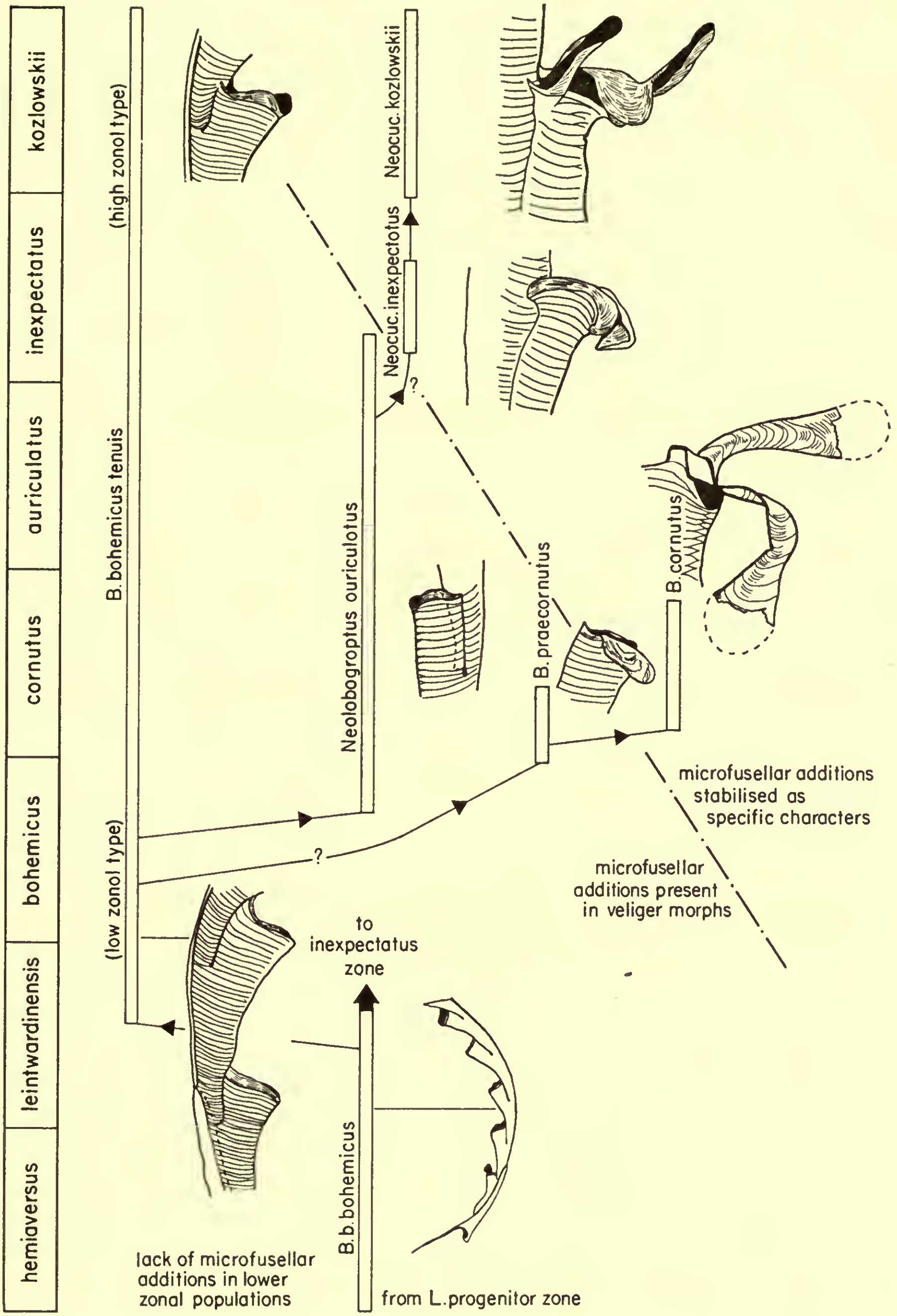

hemiaversus
leintwardinensis
bohemicus
cornutus
auriculatus
inexpectatus
kozlowskii
(low zonal type)
B.bohemicus tenuis
(high zonal type)
Neolobograptus auriculatus
Neocuc. inexpectatus
Neocuc. kozlowskii
?
?
B.praecornutus
B.cornutus
microfusellar additions stabilised as specific characters
microfusellar additions present in veliger morphs
to inexpectatus zone
B.b.bohemicus
lack of microfusellar additions in lower zonal populations
from L.progenitor zone

FIG. 45. Evolution of *Bohemograptus*, *Neolobograptus* and *Neocucullograptus*, simplified and redrawn after Urbanek (1970). Figures approx. × 27.

44. *Bohemograptus*. The research of Urbanek (1970) has demonstrated that the *B. bohemicus* (Barrande) lineage extends well above the *leintwardinensis* Zone, and leads eventually (in pre-*ultimus* Zone strata) to the genus *Neolobograptus* (below) and to *Bohemograptus cornutus* Urbanek and species of *Neocucullograptus* in which the microfusellar additions become stabilized as specific characters (Fig. 45). *Bohemograptus* is characterized by ventrally curved species with modified pristiograptid thecae the apertures of which may be devoid of or provided with microfusellar additions as lobate, annular or tape-like structures. The roots of the genus probably lie among the low Ludlow pristiograptids, evolving by gracilization of a member of the main stock and the production of a ventrally curved rhabdosome. It is of interest that *B. bohemicus* appears low in the *nilssoni* Zone and yet not until post-*leintwardinensis* times does the evolutionary burst take place, thus providing a pattern parallel with monoclimacid and pristiograptid gross evolution (Fig. 1).

45. *Neocucullograptus* and *Neolobograptus*. *Neolobograptus auriculatus* Urbanek is the species of a monotypic genus providing the link between *Bohemograptus* and *Neocucullograptus*. Additions of microfusellar apertural structures had not yet become stabilized, but the genus differs from *Bohemograptus* in having strong bilateral elevations (lappets) of the thecal margin provided with dorsolateral incisions (Fig. 45).

Neocucullograptus evolved directly from the previous species and is characterized by advanced microfusellar apparatus (Fig. 45).

46. *Neodiversograptus* Urbanek (1963) has been discussed in great detail by that author and by Palmer (1971) and more briefly by Rickards (1973) in his re-examination of *Diversograptus* Manck. The genus evolved in the low Ludlow in much the same way as *Bohemograptus*, namely by gracilization of a member of the pristiograptid stock, but in this case producing species capable of cladia generation from the sicula (Fig. 46). These eventually gave rise to the genus *Linograptus* (below).

47. *Cucullograptus* and *Lobograptus*. The definition and evolution of these genera were described by Urbanek (1966). *Lobograptus* was essentially a simpler cucullograptid originating in the same way as *N. nilssoni* in the low Ludlow. The earliest species is *L. progenitor* giving rise to *L. simplex* and then *L. expectatus*, each with symmetrical apertural processes. Eventually lobograptids such as *L. scanicus* and *L. imitator* evolved with hypertropy of the right apertural lobe ; finally *L. cirrifer* evolved with a rostral superstructure on the apertural lobes.

Cucullograptids evolved from *L. simplex* (Fig. 47) but exhibit hypertrophy of the left lobe (e.g. *C. pazdroi*), eventually acquiring a rostral superstructure on the apertural lobes (*C. aversus rostratus*).

48. *Linograptus* and *Abeisgraptus*. The Devonian genus *Abeisgraptus* Hundt probably evolved from the late Silurian–early Devonian genus *Linograptus* Frech, by the development of paired thecal cladia on the procladium and central sicular

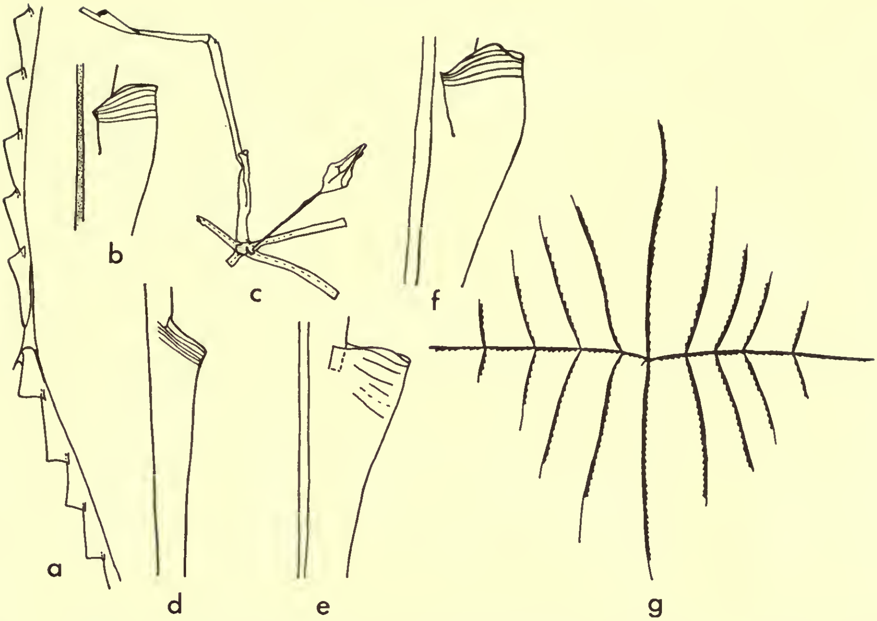


FIG. 46. Nature of thecae and cladia in *Neodiversograptus*, *Linograptus* and *Abeisgraptus*: a, *N. nilssoni*, after Palmer (1971), ×6 approx.; b, *Linograptus posthumus*, proximal theca, simplified after Urbanek (1963), ×12½; c, *Linograptus posthumus*, after Urbanek (1963), ×7 approx.; d, *Neodiversograptus beklemishevi*, after Urbanek (1963), proximal theca, ×12½; e, *N. beklemishevi*, after Urbanek (1963), distal theca, ×12½; f, *Linograptus posthumus*, distal thecae, after Urbanek (1963), ×25; g, *Abeisgraptus tenuiramosus*, after Jaeger (1959), ×1 approx.

cladium (Fig. 46). *Linograptus* has no thecal cladia, but at least one and usually several sicular cladia.

VI. SUMMARY OF SILURIAN TRENDS

From the detailed lineages described in sections III to V above (pp. 11–83) it is possible to identify a number of 'trends', morphological changes, often affecting several distinct evolutionary lineages, biserial *and* uniserial, and quite commonly affecting them at almost the same time or for a similar span of time. The more important or conspicuous of these are summarized below. It has often been found that the *recognition* of a new morphological feature in one group has been followed rapidly by its recognition in others. A good example is that of genicular hoods of microfusellar tissue first noted in monograptids by Urbanek (1958), although known in biserials as early as 1890 (Holm), and now known in other monograptid groups in the Llandovery and Ludlow and in biserials in the Llandovery. Fig. 48 is an attempt to note the first appearance, acme and span of the main trends discussed. It is not the purpose of this paper to explain the various Silurian trends in terms of the mode of life of graptoloids, but clearly the many new features described above have some import on the question. An interpretation in terms of mode of life will be made elsewhere.

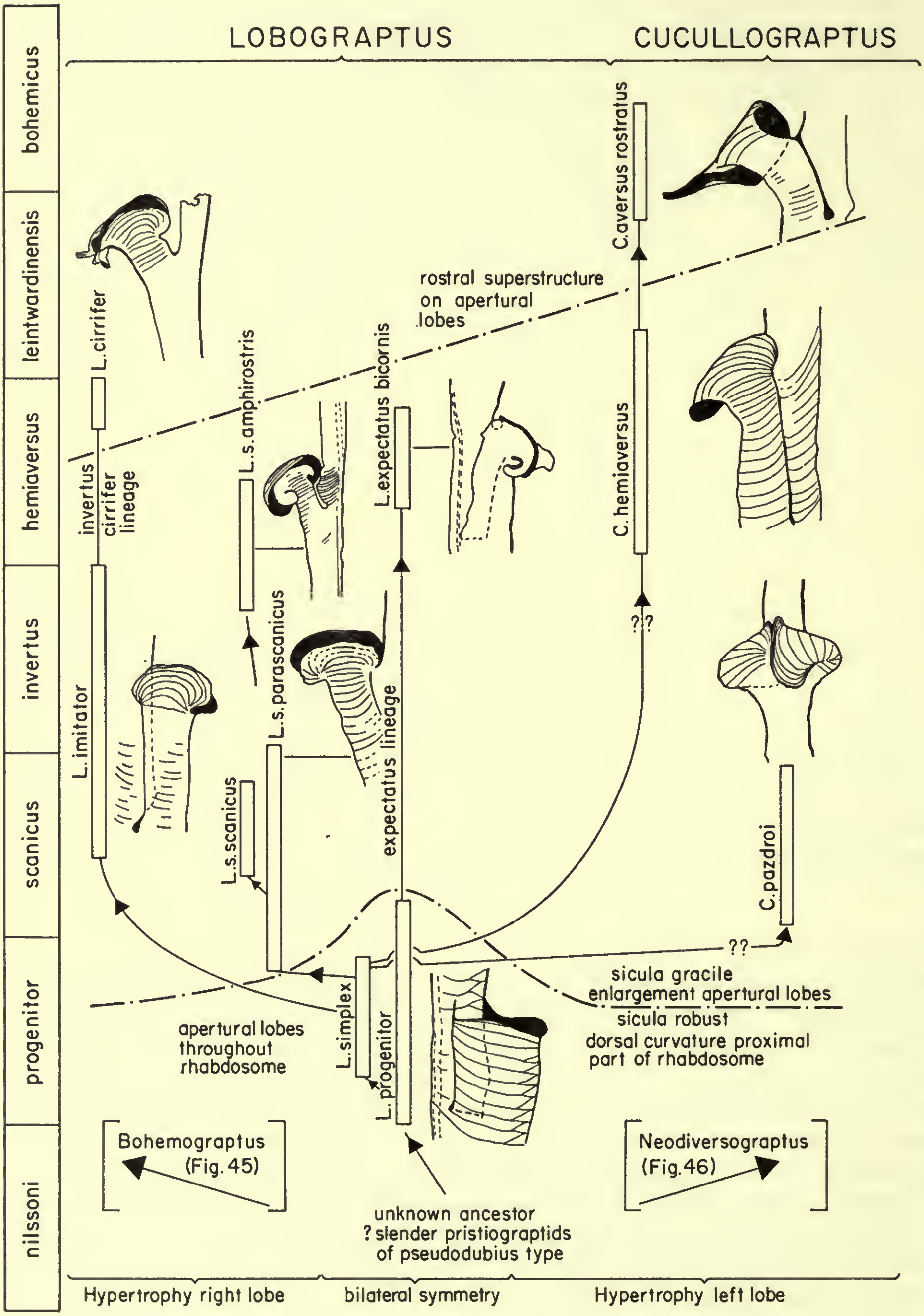

LOBOGRAPTUS
CUCULLOGRAPTUS
bohemicus
leintwardinensis
hemiaversus
invertus
scanicus
progenitor
nilssoni
C.aversus rostratus
rostral superstructure on apertural lobes
L.cirrifer
L.s.amphirostris
L.expectatus bicornis
C.hemiaversus
invertus cirrifer lineage
L.imitator
L.s.parascanicus
expectatus lineage
??
L.s.scanicus
C.pazdroi
??
sicula gracile
enlargement apertural lobes
sicula robust
dorsal curvature proximal part of rhabdosome
apertural lobes throughout rhabdosome
L.simplex
L. progenitor
Bohemograptus (Fig. 45)
Neodiversograptus (Fig.46)
unknown ancestor ?slender pristiograptids of pseudodubius type
Hypertrophy right lobe
bilateral symmetry
Hypertrophy left lobe

FIG. 47. Evolution of *Cucullograptus* (*Cucullograptus*) and *C.* (*Lobograptus*), simplified and redrawn after Urbanek (1966). Figures approx. × 27.

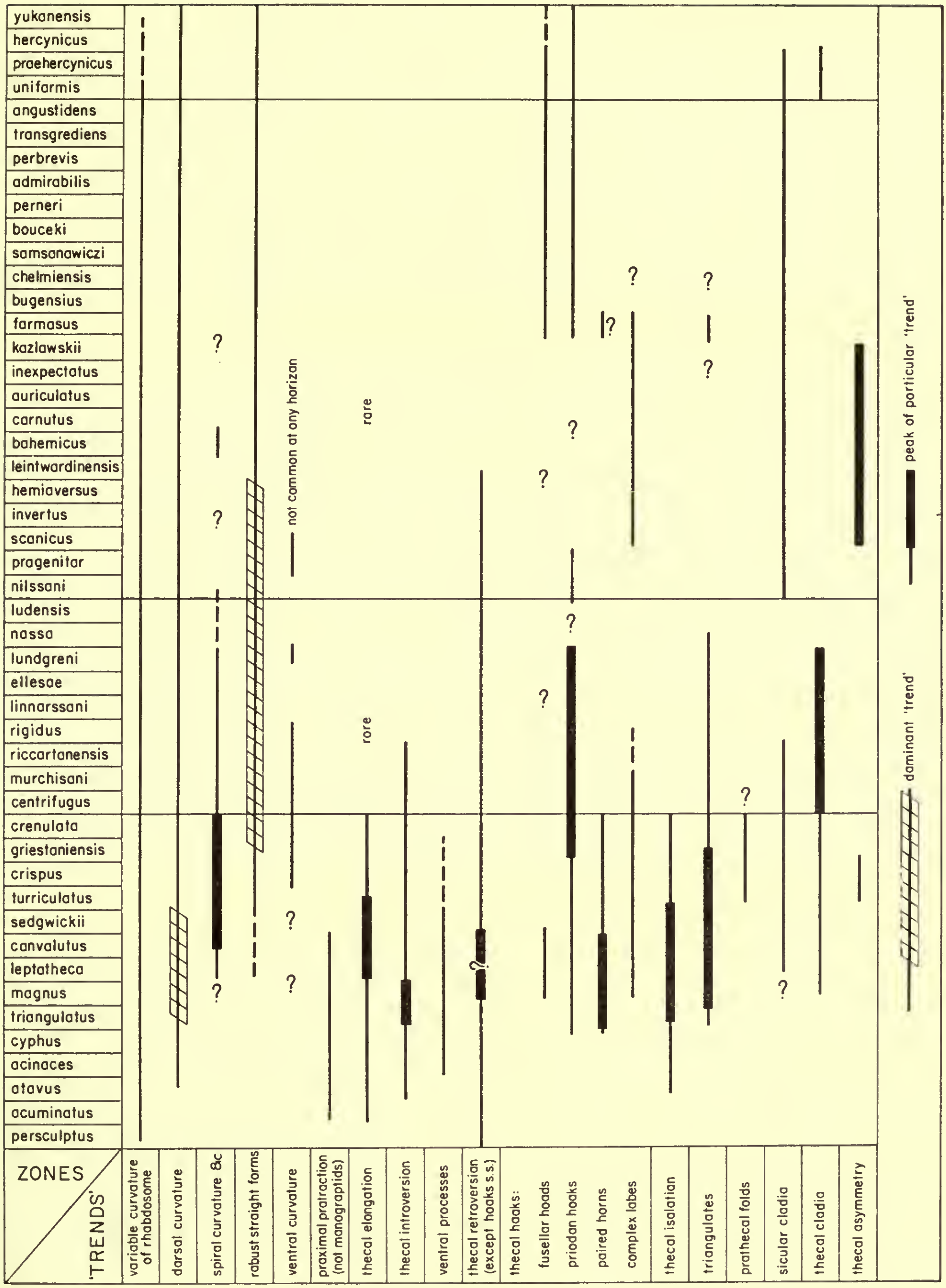


FIG. 48. Summary of the geological range, peaks and dominance of 'trends' (pp. 83–96).

Variable Rhabdosome Curvature

Biserial scandent graptoloids such as *Glyptograptus* have stiff rhabdosomes but on achieving proximal protraction, in the form of the dimorphograptid or monograptid condition, the rhabdosome immediately becomes curved in some way. The earliest monograptids (Fig. 17, p. 37) tend to be long, slender and variously curved. Thus *Atavograptus* species and early *Pribylograptus* species such as *P.* cf. *incommodus, P. sandersoni* and *P. incommodus* have these attributes, as do the gracile members of many later (mostly robust) graptolite groups. Even a few robust species like *Pribylograptus leptotheca* are either dorsally or ventrally curved, or both, and these may be regarded as having to some extent retained the earlier state.

Dorsally Curved and Spiral Rhabdosomes

At an early stage in monograptid evolution some rhabdosomes assumed a more or less stiff dorsal curvature (Fig. 17). The genus *Coronograptus,* which originated in the *atavus* Zone (Fig. 17), becomes either stiffly or pronouncedly dorsally curved and the rhabdosomes robust, whilst *Lagarograptus,* appearing shortly after in the *acinaces* Zone, is less robust and with a less stiff dorsal curvature. It seems to be true that the more robust graptolite species were stiffly curved, usually dorsally. Each group has one or two exceptions: *Monoclimacis continens* Törnquist and *Testograptus testis* Barrande are examples.

Pribylograptids achieved dorsal curvature with *P. argutus* in the *cyphus* Zone and dimorphograptids almost immediately (in the uniserial portion), although the earliest form, *D. elongatus,* does not always display a dorsally curved uniserial portion. In the case of dimorphograptids the presence of dorsal curvature in even quite short uniserial portions probably reflects the immediate adjustment of a vertically oriented biserial graptolite in order to maintain its vertical position in the water (Figs 49a–c). Thereafter probably most monograptid graptolites were

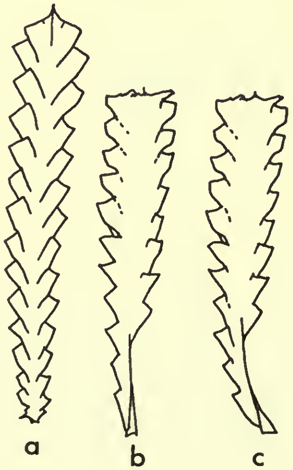


Fig. 49. Comparison of the maximum curvature seen in a fully biserial scandent species, *Orthograptus truncatus* Lapworth, (a) with that seen in the proximal end of *Dimorphograptus* (c): the situation in *D. erectus* (b), that is with a relatively straight uniserial portion, is quite unusual, and even in these cases some overall curvature is imparted by the position of the sicula. It is suggested that the curvature of the uniserial portion is an attempt to hold the centre of gravity so that the rhabdosome remains oriented vertically in the water. ×5.

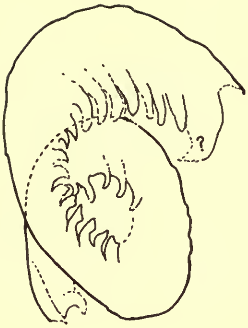


Fig. 50. *Monograptus discus* Törnquist, HUR S231,2/62, after Rickards (1970), showing a common form of preservation of the species indicating that even in short rhabdosomes curvatuve may have been helical rather than plane spiral. × 10.

dorsally curved (e.g. *Rastrites*, '*Demirastrites*', '*Campograptus*' etc.) until about the *sedgwickii* or *convolutus* Zone when the proportions of other curvatures increased, including spiral rhabdosomes.

Very little research has been done on spiral rhabdosomes like those of *M. turriculatus* and *Cyrtograptus murchisoni*, but in all probability a good number of dorsally (and ventrally) curved rhabdosomes were actually conical spirals in life. *M. discus* (Fig. 50; Pl. 3, fig. 3) is one of the shortest, robust, ventrally curved species known yet the frequency with which the proximal end is found covering over the mesial portion strongly suggests a spiral rhabdosome arrangement, as do the preservational attitudes of many rastritids and demirastritids. We know of no cases where a plane spiral rhabdosome has been established, except possibly *M. convolutus* Hisinger or *T. testis* (Barrande).

It has been pointed out above (p. 73) that rhabdosomal curvature is of little guide to specific affinities, and it can be stated that most groups or genera (established on detailed *thecal* structure) usually have members which are dorsally curved and a few which are ventrally curved, or yet others which are more or less straight. However, in terms of broad evolution, the following stages were reached in the following order.

1, variously curved, slim rhabdosomes (often seen again in the gracile members of most groups).

2, dorsal curvature achieved in the *atavus* Zone and whilst maintained into the Devonian, dominant in the *triangulatus* to *sedgwickii* Zones.

3, from the *convolutus* or *sedgwickii* Zones upwards to the low Wenlock many spiral and many straight rhabdosomes occur (*Monograptus* s.s. and *Monoclimacis*).

4, from low Wenlock upwards straight monograptids, often with *slight* curvature, dominated.

5, in the Ludlow and above there are again slender and variously curved types (e.g. *M. microdon*), but also many stiff and more or less straight forms.

Ventrally Curved Rhabdosomes

These are in a minority in most groups and do not appear with certainty until post-*sedgwickii* strata (e.g. '*Streptograptus*'), although some earlier spiral rhabdosomes may have essentially ventral curvature (i.e. with the thecae facing inwards within the cone as in conical dendroids) : *M. involutus* is a possible early example (*magnus–sedgwickii* Zones) and *M. turriculatus* and *M. discus* are certainly later ones. After the upper Llandovery they are uncommon. Slight proximal region ventral curvature is characteristic of many pristiograptids in the Ludlow and Pridoli, as well as in some other groups. The Pridoli species *M. helicoideus* is markedly coiled.

Proximal Protraction

Many Llandovery biserial graptolites, except retiolitids, had a tendency to produce protracted proximal ends either by achieving the dimorphograptid condition, or by lengthening the early thecae and sicula and drawing out the proximal end into a thorn-like point. The first occurrence is in the *acuminatus* Zone with *Akidograptus ascensus* and *Orthograptus* ? *acuminatus* which achieve the result by the second method (Fig. 7, p. 19). Strictly speaking the monograptid condition itself is an example of extreme protraction, and this first occurred in the *persculptus* Zone with *Atavograptus ceryx*, a possible member of dithyrial populations.

The dimorphograptids and many monograptids appear in the *atavus* Zone, and *Rhaphidograptus toernquisti* (Fig. 8h, p. 22) may be considered a dimorphograptid with a uniserial portion of one theca only. Subsequently the tendency declines and is last seen in the lineage *Petalograptus folium* to *Cephalograptus cometa* in the *convolutus* Zone. The tendency for many biserial groups to have tiny end members (*Pseudoclimacograptus*, *Climacograptus*) is probably a process quite unrelated to proximal protraction : in the former process the whole rhabdosome becomes minute and proximal protraction only takes place secondarily and in terms of absolute measurement, *not* in relation to the rest of the rhabdosome.

Thecal Elongation

The most extreme case known is that of *Cephalograptus cometa* where the thecae reach a length of 30 mm in some specimens. These are the longest graptoloid thecae on record and must exceed the length of many dendroid thecae, including those of *Coremagraptus*. Thecal elongation is, naturally, associated with the proximal end protraction discussed in the last section but also occurs in groups lacking this : *Pribylograptus leptotheca*, *Rastrites maximus*, *Lagarograptus acinaces* and *Monograptus singularis*. Mostly it is a Llandovery feature, with its acme in the middle of the Llandovery (*leptotheca* to *maximus* Zones), but is also known in Ludlow pristograptids (*M. butovicensis* Bouček and *M. egregius* Urbanek), whilst lobograptids have elongate necks prior to the apertural apparatus.

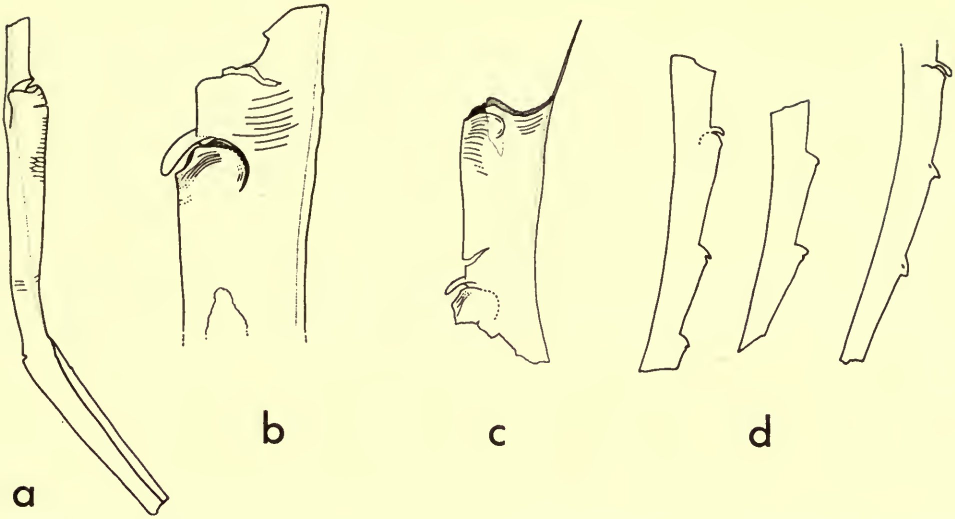


FIG. 51. a–d, *Monograptus* sp., after Hutt *et al.* (1970), showing combination of paired, lateral thecal lappets and genicular hood, the possible basic requirements for derivation of some *Monograptus* s.s. from *Monoclimacis*; Riksmuseum Cn 54882–8; a–c, × 45 approx., d, × 15.

Thecal Introversion

Thecal introversion has been regarded previously as a typically Ordovician feature, but it appears in the Silurian with *Pribylograptus* cf. *incommodus* (Fig. 17, p. 37) in the *atavus* Zone. Introversion in the form of paired horns and genicular hoods is confined to the genus *Pribylograptus* ranging from the *atavus* to the *sedgwickii* Zones, and to the biform *M. sudburiae* group (p. 45) from the *cyphus* and *triangulatus* Zones. *Barrandeograptus pulchellus* (Bouček & Přibyl 1954) from the *crenulata* to *riccartonensis* Zones almost certainly has introverted thecae but the structure has not been fully ascertained. Otherwise thecal introversion is seen in *Monograptus* sp. 2 (Hutt *et al.* 1970) and in *Glyptograptus* (*Pseudoglyptograptus*) spp. 1 & 2 (Rickards 1972). The former, from the *gregarius* Zone, may be related to *Pribylograptus* in that the introversion takes the form of paired lateral lappets (which may be flattened, open tubes) and a median, ventral, apertural saddle beneath a genicular hood. *G.* (*Pseudoglyptograptus*) has essentially everted thecae (p. 22) but the apertural margins in some (Fig. 8f) have a pronounced median process and paired lateral incisions: the ventral process itself has a slight saddle not unlike that in *Monograptus* sp. 2 (Fig. 51). The effect of this structure is to impose an effectively introverted aspect on the apertural regions only of a thecal tube which as a whole is sinuous and everted. This occurs in *G.* (*Pseudoglyptograptus*) in the *triangulatus* and *magnus* Zones, that is at about the acme of thecal introversion in *Pribylograptus*. The only later pseudoglyptograptid of which we are aware, *G.* (*P.*) *tabukensis* Rickards & Koren' from the *convolutus* Zone, does not display apertural introversion.

Ventral Thecal Processes

Unless one includes the ventral apertural processes of *G.* (*Pseudoglyptograptus*) these structures are at present known only in *Lagarograptus*, first appear with *L. acinaces* in the *acinaces* Zone and range up to the *sedgwickii* Zone with *L. tenuis* (Fig. 17, p. 37). They are perhaps best considered as attempts to simulate thecal 'hooks' which, at these horizons, are found in a wide variety of graptoloid groups. Hence the genicular hood can be explained as a protective device over the essentially everted thecal zooid (Fig. 17). The nearest approach in other groups to the elongate ventral apertural processes of *Lagarograptus* is a slight outrolling of the ventral thecal lip, a feature clearly evolved to facilitate movement of the zooid itself into an extrovert position and similarly for it to retract with smoothness and speed.

Retroversion

Retroversion is here considered separately from thecal hooks (below) because various structures essentially simulative of them occur in groups without true thecal hooks. The sigmoidal curvature of the thecal tube in *Cystograptus*, *G.* (*Pseudoglyptograptus*) and *P.* (*Clinoclimacograptus*), coupled with eversion of the apertural margin, gives an overall eversion to the thecae. The zooid presumably faced outwards or ventrally during extroversion, in contrast to the ancestors of these groups where the zooid probably faced distally. Eversion to this degree (Fig. 3c, p. 14) compares with the similar eversion in *Monoclimacis* (Fig. 24, p. 55) which may be regarded morphologically and evolutionally as an early version of a thecal hook. The tendency therefore is towards eversion leading to retroversion in several groups other than monograptids. The presence of genicular hoods in other genera may be interpreted similarly: the result for the extroverted zooid would be to face ventrally or proximally as in, for example, *Climacograptus innotatus*. In others, such as *P.* (*Metaclimacograptus*) *undulatus* (Figs 3e, 4a, pp. 14–15) the situation would appear to be more flexible since the mesial part of the genicular hood is less developed and the zooid could therefore face either ventrodistally or ventroproximally. Thus the result of all these modifications can be interpreted as a *tendency towards*, if not actually achieving, the hooked condition typical of many monograptids which became, of course, the more successful group.

Thecal retroversion as interpreted above first appears with *C. innotatus* and *R. toernquisti* in the *acuminatus* Zone, and ends (monograptids excluded) with *Holoretiolites* in the Ludlow (Fig. 16, p. 35).

Thecal Hooks

It has been pointed out by Hutt *et al.* (1972) that thecal hooks can be considered in eight different forms. Three of these have been considered above (in the sections on ventral apertural processes and retroversion, above) and the remainder are enumerated as follows.

1, genicular hoods of fusellar tissue, that is growth of the dorsal thecal wall but not of the lateral or ventral walls.

2, the *priodon* type hook.
3, paired horns by development of the dorsal thecal margin.
4, more complex hooks and lobes of fusellar tissue.
5, each of the foregoing could be theoretically developed as microfusellar tissue or alternations of both fusellar and microfusellar tissue.

The appearance of these hooks is included in Fig. 48, p. 85. *Priodon* style hooks may slightly precede, in the form of *M. austerus austerus* (Fig. 19, p. 43), the incoming of paired, retroverted horns exemplified by *M. austerus bicornis* in the top of the *cyphus* Zone. Genicular hoods of fusellar tissue also appear quite low in the Llandovery (e.g. *M.* sp. 1 of Hutt *et al.* 1970, *gregarius* Zone) and are still present in Devonian monograptids, although of an independent origin (p. 79). More complex lobes and hooks appear with *Monograptus* sp. B (Fig. 26) in the *magnus* Zone of the Lake District and, again, are found in the Ludlow derived from quite different ancestors. The fifth, theoretical, possibility has to be considered in view of Urbanek's (1970) work, but at present such structures are only known in Ludlow graptolites. With the exception of the fifth category, therefore, all hooks appear low in the Llandovery, and because of this, and their widespread occurrence in different groups, they may be regarded as one of the most typical of all Silurian features.

Thecal Isolation

The earliest instance of metathecal isolation, again a typically Silurian feature, is *Dimorphograptus decussatus* from the *acinaces* Zone. In this species as in other dimorphograptids the actual nature of the aperture has not been elucidated but in profile at least the thecae of the uniserial part and the proximal thecae of the biserial part appear to have isolated apertures : more distally the thecae have the normal biserial arrangement. As far as we know, the isolation achieved by the proximal thecae of the biserial portion in *D. decussatus* is the only instance of biserial thecal isolation.

The most well-known instances of metathecal isolation are to be found in the 'demirastritids' and *Rastrites* species where the metathecal tubes of the thecae grow at right angles to the main growth direction of the rhabdosome and develop from extremely slender prothecal tubes (which Schauer (1967) incorrectly terms the virgula). Isolation of this kind is seen as high as the *griestoniensis* and *crenulata* Zones where the 'demirastritids' die out. The last known *Rastrites* species are in the *turriculatus* Zone.

However, metathecal isolation is also seen (Fig. 26) in non-rastritiform monograptids such as the long-ranging *M.* sp. of Hutt (p. 58). In this species the prothecal tube is just as slender as in *Rastrites* but the metathecal portion, instead of standing at a high angle to the rhabdosome, actually forms a fairly normal *priodon*-like hook on a much expanded late prothecal tube.

In a sense metathecal isolation is also achieved by the *M. knockensis*–*M. singularis* line even though the late metathecal part, and thus the aperture itself, doubles back and faces the prothecal tube (Fig. 27, p. 59). *Coronograptus* *gregarius* occasionally exhibits late metathecal isolation, but it is not normally a feature displayed by graptolites with simple thecal tubes: all the above forms except *C. gregarius* and *D. decussatus* have 'hooked' thecae of some kind. The acme, judging on number of species, is about the *triangulatus* to *sedgwickii* Zones, perhaps slightly towards the bottom end of this range.

Thecal Triangulation

The importance of triangulate monograptids in the evolution of Llandovery graptolites was admirably demonstrated by Sudbury (1958). Her suggested lineages and others are described above on pages 42, 44, and 45–47: although typical of several groups, on present knowledge thecal triangulation is restricted to the monograptids and like true thecal hooks is one of the few trends so restricted. Moreover the groups affected may well be quite closely related genetically and have their origins in the *M. austerus* group. The earliest species showing any kind of thecal triangulation is *M. difformis* which Hutt (1974) has established as being a top *cyphus* Zone species probably possessing simple thecal hooks. The mesial thecae of *M. difformis* are distinctly triangular (Fig. 19, p. 43). This is of considerable interest in that we normally think of new characters being introduced either proximally or distally: in the case of the triangulate monograptids it is said that the proximal introduction and spread of isolated thecae results eventually in *Rastrites* (p. 47). But triangulate monograptids such as *M. triangulatus* and *M. fimbriatus* invariably have at least one axially elongate non-triangular theca at the proximal end. Thus thecal triangulation is almost certainly directly related to the acquiring of a strong dorsal curvature by the rhabdosome, the triangular thecae first appearing at the point of maximum curvature and spreading *proximally and distally* as the curvature increases. Such arguments cannot be applied to thecal isolation which occurs in more or less straight species such as *M. capulus* and *R. equidistans spengillensis*.

The range in time of triangular thecae is from the top of the *cyphus* Zone to the *crenulata* Zone, but continues in modified form in species of *Cyrtograptus* throughout the Wenlock. Subsequently triangular thecae reappear as *M. formosus* (Fig. 37, p. 72) in the *ultimus* Zone of the Pridoli and although the origin may be quite different (p. 78) the reason may be the same, namely the acquisition of a strong dorsal curvature by the rhabdosome, particularly in its mesial regions. It is difficult to define an acme for the triangulate monograptids since, unlike those species exhibiting thecal isolation, they span a longer period, but undoubtedly triangulation is more widespread in the Llandovery than later.

Gracile and robust rhabdosomes

A common tendency amongst monograptid groups in particular is to produce both very slender and very robust rhabdosomes, the former commonly just after the inception of the group and the latter more commonly at a later date. In other words groups or genera often have more relatively slender species at the beginning of a lineage, the later representatives being generally more robust. The *lobiferus* lineage forms a good example originating through *M. undulatus* and *M.* sp. A (Fig. 26, p. 57) from the slender *Atavograptus*, but eventually leading to *M. lobiferus, M. knockensis* etc. Similarly the *priodon* lineage is represented in the Wenlock by several broad species including a form of *M. flemingii* with a dorso-ventral width of well over 4 mm (Bulman 1965). Early forms of *M. priodon* are commonly quite slender (*M. parapriodon*) and the origins of the genus probably lie in slender forms of *Monoclimacis*, a genus also producing more robust species in the Wenlock than in the Llandovery. However, the *priodon* lineage does produce at an early stage (*turriculatus* to *griestoniensis* Zones) extremely robust graptolites such as *M.* sp. A of Bassett & Rickards (1971) which might easily be confused, in a monotypic collection, for the Wenlock species *M. flemingii.* By way of contrast the *lobiferus* lineage evolved *M.* sp. B, a most slender and well-advanced form (Fig. 26, p. 57) at the very beginning of the line (*magnus* Zone). *M. gracilis* is an early offshoot of the *Atavograptus* lineage (Fig. 17, p. 000) whilst *M. angustus* and *M. fragilis* are probably similarly referable to the genera *Pribylograptus* and *Atavograptus* (or *Pristiograptus*) respectively.

However, the above 'rules' are not absolute and there is also an undoubted tendency, well displayed by the *Pristiograptus dubius* line, to evolve short-lived slender and broad species at fairly regular intervals throughout the long range of the species from the *riccartonensis* Zone into the Ludlow. Even *Pristiograptus*, however, originates through slender species and tends to produce its most robust species in the Wenlock and Ludlow: it is of interest that the few Ludlow *slender* 'pristiograptids' should have been capable of such spectacular evolution (Figs 45–47 and pp. 82–83). *Monograptus* and *Monoclimacis* both originate from relatively slender species, secondarily produce slender species high in the Llandovery ('*Mediograptus*' and *M. griestoniensis*) and reach a peak of robustness in the Wenlock. The triangulate monograptid plexus may display similar tendencies to those described above.

Another example of the general pattern of early species in a lineage to be somewhat more slender than the later is seen in the *angustidens–uniformis* and *hercynicus* group lineages. The early members of the *angustidens–uniformis* group (*M. balticus* Teller, *M. angustidens* Přibyl and forms closely similar to it) are more slender than *M. uniformis*. Similarly, the early members of the *M. hercynicus* group (*M. birchensis* Berry & Murphy and *M. praehercynicus* Jaeger) are more slender than *M. hercynicus hercynicus* Perner and *M. hercynicus nevadensis* Berry. Berry & Murphy (1974) have documented the stratigraphic ranges of the slender and more robust members of the *hercynicus* group in Nevada, and Jackson & Lenz (1972) have indicated the stratigraphic ranges of the gracile and robust members of the *angustidens–uniformis* group in the Yukon, Canada. In addition, the oldest representatives of the *P. transgrediens* group (*P. bugensis* Teller and *P. chelmiensis* Teller) are more slender than the later members of that group (*P. transgrediens transgrediens* Perner). The generalized trend towards robust forms from gracile members early in the history of a lineage continues among Pridoli and early Devonian stocks, although there are exceptions to the general trend (such as *M. telleri* Lenz & Jackson among *hercynicus* group members).

Prothecal Folds

Prothecal folds are a typical Ordovician structure occurring, for example, in a number of didymograptid (*sensu lato*) types and in some *Dicellograptus* species, but homologous structures have recently been discovered in Silurian monograptids (Hutt *et al.* 1970). In uniserial scandent species the dorsal wall of the rhabdosome is marked by the nema : this is not involved in the prothecal fold but the prothecal tube forms paired bulges to each side of the nema (Fig. 37, p. 72) as well as betraying a distinct kink or bulge in the ventral wall. At present prothecal folds are known in such species as *M. exiguus* which, based on the nature of the apertural hook, has similarities to *M. spiralis*, and in *M. nodifer* and possibly other 'streptograptids' and 'mediograptids'. Thus the feature may occur in different groups at about the same time, namely *turriculatus* Zone to basal Wenlock, but as yet no evolutionary significance has been detected. The Silurian prothecal folds must, however, have originated independently in the Silurian and cannot have been derived from Ordovician dicellograptids possessing analogous structures. Undoubtedly more species will be found to exhibit prothecal folds when satisfactorily preserved material is to hand : at the moment the known species are slender, with 'hooked' thecae, and have either strong ventral or strong dorsal curvature.

Thecal and Sicular Spinosity

The relatively late members of many Silurian lineages display thecal spines. For example, it has been suggested above (p. 49) that *M. sedgwickii* evolved from a triangulate monograptid ancestor by straightening of the rhabdosome and development of thecal spines : *M. halli* the suggested successor to *M. sedgwickii* displays a degeneration of the same basic structure. Similarly *M. pseudoplanus* displays paired horns or tubes which in the suggested descendant (Sudbury 1958) have degenerated to very short spines. Other late triangulates also develop long spines (*M. delicatulus*, Fig. 38, p. 73) as do some of their derivatives towards the end of *their* lineages (*M. turriculatus, M. spiralis, R. phleoides*). Indeed in those species belonging essentially to the triangulate monograptid plexus long spines are usually achieved in the *convolutus* and *sedgwickii* Zones and thereafter degenerate : the exception, *M. spiralis*, may well have evolved further into *Cyrtograptus* species in which the long spines became the pseudovirgulae of the cladia.

The *Monograptus* s.s. group most certainly developed spines in its later species such as *M. flemingii*, and these developed from the dorsolateral apertural processes of earlier species such as *M. marri* and *M. priodon*. However, the *priodon* line not only developed extremely robust rhabdosomes (*M.* sp. A of Bassett & Rickards 1971) at a quite early stage but these also exhibited considerable thecal spinosity and as far as is known at present had no successors with degenerative spines.

The genera *Orthograptus* and *Glyptograptus* also evolved thecal spines, again essentially in the later species, although in the case of *Glyptograptus serratus barbatus* and '*Comograptus*' *comatus* they are restricted to the proximal thecae and are strongly pendant and perhaps not all apertural in origin. In *G. serratus barbatus* there are undoubtedly sicular (apertural) spines also, as in some species of *G.* (*Pseudoglyptograptus*) (Rickards & Koren' 1974). The spinosity of these genera is achieved in the *magnus* to *convolutus* Zones, that is rather earlier than in the triangulate monograptids, which in turn is earlier than in the *Monograptus* s.s. species.

A majority of Silurian graptoloid groups did not produce spinose species, and the spinose 'thecae' of some retiolitids are too little known to be commented upon further at present.

Sicular Cladia

Sicular cladia first appear quite low in the Llandovery (possibly *magnus* Zone) in *Diversograptus* species (Rickards 1973) and occur in the upper Llandovery in *Diversograptus*, *Sinodiversograptus* and probably *Barrandeograptus*, the last ranging up into the Wenlock (p. 72). Although in regenerated, bipolar rhabdosomes the nema is also regenerated to grow along the dorsal wall of the new stipe, in the above genera the dorsal wall presumably lacks a nema since the virgella is enclosed in the *ventral* wall of the first theca of the new stipe, and there is no evidence at present of a dorsal sicular spine having been produced. The latter is, however, a possibility.

No other groups with sicular cladia have been detected in the Wenlock, *Barrandeograptus pulchellus* being essentially a survival from the Llandovery, and sicular cladia are not seen again until the genera *Neodiversograptus*, *Linograptus* and *Abeisgraptus* which span the low Ludlow to low Devonian. These three genera are closely related (Urbanek 1963) but are quite removed genetically from the high Llandovery genera just discussed. In the late Silurian forms a dorsal sicula spine or spines forms the dorsal edge of the new stipe or stipes whilst the sicular aperture usually remains open. The late Silurian and Devonian genera form an undoubted lineage, but the status of the Llandovery genera *Diversograptus* and *Sinodiversograptus* has recently been called into question by Rickards (1973) who found sicular cladia in a number of quite different Llandovery groups and concluded that the feature was a late stage of astogeny potentially achievable by many groups.

Thecal Cladia

The presence of thecal cladia in the genera *Diversograptus*, *Sinodiversograptus* and *Barrandeograptus* confers upon them a value not given by the mere presence of sicular cladia, but the possibility does remain that these also are potential late astogenetic growth stages of several groups. The genus *Cyrtograptus*, however, originating in the highest Llandovery strata (Bouček 1933 ; Jackson & Etherington 1969), forms a sizeable evolutionary plexus in the Wenlock with several (poorly studied) main lineages (p. 76) : there are no accompanying, similar graptolites *without* cladia as commonly the case in the upper Llandovery with *Diversograptus* etc. The same arguments that are applied to *Cyrtograptus* may also be applied to the early Devonian *Abeisgraptus* which is the next genus to exhibit thecal cladia. Thus all three groups originated quite independently, at different times, and each probably has a quite different evolutionary status and value. There are few *Abeisgraptus* species, and many *Cyrtograptus* species.

Thecal Asymmetry

Despite the common assertions of Elles & Wood (1901–18) of thecal asymmetry in Silurian monograptids the only records of which we are aware are *M. proteus* Barrande in the Llandovery (Hutt *et al.* 1970) and the Ludlow species of *Cucullograptus* (1966) and *Bohemograptus* (1970) described by Urbanek. The latter genera have asymmetrical development of processes or of the lateral apertural thecal lappets, whilst *M. proteus* displays a pronounced torsion of the thecal axis (Fig. 52). Thus only the asymmetry described by Urbanek falls into a clear evolutionary setting, and we suggest that on present evidence *M. proteus* represents a single, unusual side line of the triangulate monograptid lineage from *M. pseudoplanus* (Sudbury 1958) to *M. planus.*

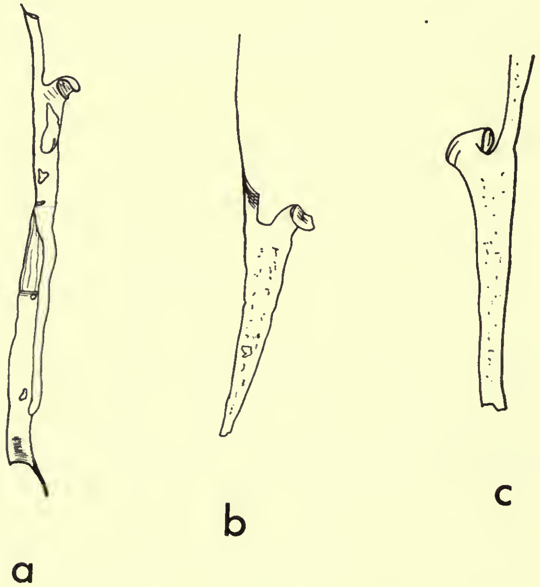


FIG. 52. a–c, *Monograptus proteus* (Barrande), Riksmuseum Cn 54934–6, ×40, after Hutt *et al.* (1970), showing the only known case of pre-Ludlow thecal asymmetry, and the only case involving torsion of the thecal axis.

VII. SYSTEMATIC SECTION

The classification of graptoloids has been extensively discussed in recent years and authoritative papers published by Bulman (1955, 1963, 1970) and Jaanusson (1960) in particular. There has been a large measure of agreement concerning the classification of Silurian graptoloids, with perhaps the greatest discrepancy of views on the subject of the classification of *Monograptus.* Recent approaches to this particular problem have been described by Urbanek (1958) and by Bulman & Rickards (*in* Bulman 1970), whilst Rickards (in press) redefines several Llandovery graptoloid genera. In this work we have found it easy to follow the broad features of the classification of Bulman (1970), but the evolutionary studies themselves necessarily suggest some changes in detail; at the same time we have baulked at the prospect of defining several new genera for the reasons expressed above, namely that there are considerable areas, in the upper Llandovery in particular, needing a great deal of further study. We give below, in the form of systematic notes, comments upon various genera and species where we have something new to add relevant to the evolutionary story of sections III to VI. No new morphological terms are introduced; thecal spacing measurements are taken in the manner recommended by Packham (1962) in which a small number of thecae are measured and this figure translated to a 'thecae per cm' value. Location of illustrated specimens is given on the captions to the figures, both in the main text and on the plates.

Order GRAPTOLOIDEA Lapworth 1875

Genus *CLIMACOGRAPTUS* Hall 1865

Climacograptus innotatus pacificus Ruedemann 1947

(Fig. 2, p. 12)

The subspecies is clearly close to the typical subspecies in general dimensions, being rather broader (1·5 mm exclusive of spines) and having a higher thecal spacing (20 in 10 mm as compared with 15–16 in 10 mm). However, the genicular process certainly consists of a pair of spines rather than a genicular hood, and it may eventually be necessary to raise *pacificus* to specific status. The subspecies occurs in the *complanatus* Zone in N. America, probably towards the top of that zone, and it is in keeping with the ideas expressed above that a more robust form should precede the diminutive Silurian representatives of the group. Whilst it is unlikely that genicular hoods could have developed from paired genicular spines, the opposite would be quite reasonable: the genicular hood of *P. undulatus* (Figs 3, 4, pp. 14, 15) is not unlike a pair of horse-blinkers (p. 90) and ventral elongation of these two parts of the hood could certainly result in paired spines. The process would be very similar to the production of paired spines in *Saetograptus* from a basic paired lappet structure in *M. ludensis*. *C. i. pacificus*, therefore, may be an offshoot of the main *innotatus* line of evolution.

Climacograptus typicalis Hall 1865

(Fig. 2, p. 12)

The *Amplexograptus*-like thecae are clearly exhibited by the specimen illustrated, as is the pronounced genicular process and its similarity to that of *C. i. jordaniensis*.

Climacograptus nebula (Toghill & Strachan 1970)

The best-preserved specimens of this species come not from Grieston Quarry where it was first described nor from the Lake District where one of us (J. E. H.) has recently collected it, but the Howgill Fells where it is extremely abundant in the upper *turriculatus* to *griestoniensis* Zones inclusive. Both the Lake District and Howgill Fells specimens display a pronounced geniculum, to a degree that convinces us (e.g. Hutt 1974) that the species should be referred to *Climacograptus* and not doubtfully to *Glyptograptus* as was done by its authors. Whether its origins lie with *Climacograptus* or *Glyptograptus* is uncertain, but there are certainly small species of *Climacograptus* (e.g. *C. simplex*) in the *sedgwickii* Zone which might lead directly to *C. nebula*.

Genus ***PSEUDOCLIMACOGRAPTUS*** Přibyl 1948

Subgenus ***PSEUDOCLIMACOGRAPTUS*** Přibyl 1948

Pseudoclimacograptus (P.) orientalis Obut & Sobolevskaya 1966

(Fig. 3, p. 14)

Although earlier recorded from the *cyphus* and *triangulatus* Zones by Obut & Sobolevskaya (1966, 1968) and from the '*gregarius*' Zone of Dalarne by J. E. H. and R. B. R. (unpublished information ; Fig. 3) we have recently been informed by N. Sennikov of Novosibirsk that he has recorded the species in association with *A.* cf. *acuminatus* in what he presumes to be the *acuminatus* Zone. Thus it is possible that a tenuous link existed between the latest (rare) Ordovician pseudoclimacograptids and those in the Silurian. The Swedish specimens are the only ones isolated from the matrix (Fig. 3) and it is clear that they should be referred to the subgenus *P.* (*Pseudoclimacograptus*) and not to *P.* (*Metaclimacograptus*).

Subgenus ***METACLIMACOGRAPTUS*** Bulman & Rickards 1968

Pseudoclimacograptus (Metaclimacograptus) sp.

(Fig. 3, p. 14)

A relatively robust species of metaclimacograptid has been identified by one of us (R. B. R.) from the *convolutus* Zone of Qusayba, Saudi Arabia. The species is very similar to *P.* (*M.*) *undulatus* in the angular median septum and in the presence of genicular hoods. However, the genicular hoods appear to be as equally developed ventrally as ventrolaterally whilst the rhabdosome is more robust (1·2 mm approximate dorsoventral width) and the thecae more widely spaced (13 in 10 mm distally).

Genus ***AKIDOGRAPTUS*** Davies 1929

Akidograptus ascensus Davies 1929

(Fig. 7, p. 19)

Stein (1965) concluded that Bulman's (1933, 1936) interpretation of *A. ascensus*, in which he suggested loss or reduction of th1^2, was incorrect. Bulman himself tends to agree with Stein (Bulman, personal communication), but we consider that the type specimens may well have some structure resembling a reduced th1². Further work on three-dimensional or transparent material is required before the matter can be finally resolved. In any event there is no true uniserial portion, the thecal apertures alternating throughout, and the species is essentially a climacograptid with elongate proximal thecae. Other species are known, however (*A. giganteus* Yang 1964, and, indeed, *A. ascensus*, *sensu* Stein 1965), in which the distal thecae become 'dichograptid' in type, possibly implying the acquisition of diplograptid tendencies by a climacograptid stock.

Genus ***GLYPTOGRAPTUS*** Lapworth 1873

Subgenus ***GLYPTOGRAPTUS*** Lapworth 1873

Glyptograptus (G.) persculptus (Salter 1875)

(Figs 8, p. 22, and 53 ; Pl. 2, fig. 4)

As has been partly shown by Davies (1929), there is considerable variation amongst the recorded specimens of *G. persculptus* from several well-known localities. Lake District specimens, for example, although certainly at the same horizon as the Welsh specimens, seem to be rather shorter and more slender ; the Southern Uplands collections show again slight differences but in an essentially similar assemblage. Although much work needs to be done, we have singled out one form (Fig. 8a, specimen on right) because of its striking similarity to the distal thecae of *Rhaphidograptus toernquisti*. The dorsoventral width, appearance of the thecae, thecal spacing and general rhabdosomal proportions are closely similar, and it would be almost impossible to distinguish the distal thecae of the two species. In true profile, and with three-dimensional material, the thecae of *G. persculptus* s.l. have the supragenicular thecal walls inclined outwards at a slightly higher angle, whereas those on *R. toernquisti* are almost vertical.

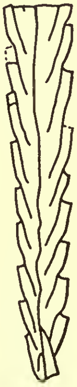


FIG. 53. *Glyptograptus persculptus* (Salter), syntype SM A20413, ×5, typical specimen from Pumpsaint, for contrast with the more slender specimens often referred to *G. persculptus* (Fig. 8, p. 22).

Glyptograptus (G.) serratus barbatus Elles & Wood 1907

This subspecies is very similar indeed to *'Comograptus' comatus* Obut & Sobolevskaya (*in* Obut, Sobolevskaya & Merkuryeva 1968). The Anglesey specimens may be slightly more robust, but have a similar thecal spacing. We agree with Elles & Wood in placing the form in the genus *Glyptograptus*, although it may eventually be shown to be specifically distinct from the coeval species *G. serratus serratus* Elles & Wood. Details of the proximal end and spinosity have not been fully established, but some of the more distal spines are certainly genicular in origin and may bifurcate, whilst at the extreme proximal end (Elles & Wood 1907 : fig. 170b) there are at least a dozen slender spines some of which may depend from the sicular aperture (Rickards & Koren' 1974).

One of us (R. B. R.) has examined the types and other specimens of '*Comograptus*' *comatus*. Many of the spines are genicular in origin, and some bifurcate, whilst the sicular aperture almost certainly has a ring of pendant spines as in *G.* (*Pseudoglyptograptus*) *rhayaderensis* Rickards & Koren' (= *G.* (*P.*) sp. 3 of Rickards 1972) and *G.* (*P.*) *tabukensis* Rickards & Koren'. Some of the distal thecae in the type specimens of '*Comograptus*' *comatus* have a concave supragenicular wall suggesting that the species *may* be referable to *G.* (*Pseudoglyptograptus*).

'*Comograptus*' *comatus* Obut & Sobolevskaya 1968

(Fig. 54)

Obut & Sobolevskaya (*in* Obut, Sobolevskaya & Merkuryeva 1968) point out that the main difference between this species and *G. s. barbatus* Elles & Wood is that the latter is more robust (up to 3·5 mm wide), longer (up to 50 mm) and with a slightly different thecal spacing (8–14 in 10 mm as against 10–12 in 10 mm in '*C.*' *comatus*). However, there is clearly considerable variation in the species of Elles & Wood (1901–18 : pl. 30, figs 11a, b) and the above differences are easily accounted for by tectonic deformation.

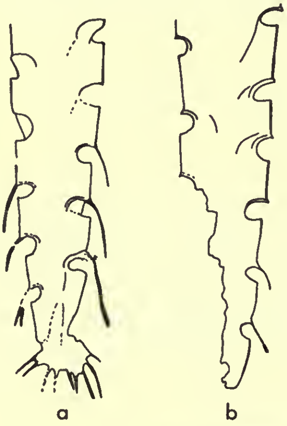


FIG. 54. a, '*Comograptus*' *comatus* after Obut & Sobolevskaya (1968). b, same, SM A79136, donated by Obut; both figures ×5.

Genus ***ORTHOGRAPTUS*** Lapworth 1873

Orthograptus mutabilis Elles & Wood 1907

(Fig. 12, p. 27)

O. mutabilis was suggested as a possible '*Dittograptus*' species by Obut & Sobolevskaya (*in* Obut, Sobolevskaya & Merkuryeva 1968), but that genus can readily be accommodated in *Orthograptus* (Rickards 1970), the only distinctive feature of *D. fortuitus* worthy of comment being the slightly rounded nature of the apertural lip not unlike that seen in some dimorphograptids. In the British Silurian rather narrower forms than that figured by Elles & Wood (1907 : pl. 29, figs 1a–c) are more common (1907 : pl. 29, fig. 1d) and such specimens from the Lake District have th^1 growing at first downwards in the manner normal for orthograptids. The specimens depicted by Elles & Wood as pl. 29, figs 1a–c resemble some continental petalograptids, and may be regarded at least as orthograptids with some petalograptid tendencies.

Orthograptus insectiformis (Nicholson 1869)

(Fig. 12, p. 27)

It has recently been shown by Hutt (1974) and Rickards & Koren' (1974) that the type specimens of this species display pronounced virgellar division similar to that described by Hutt *et al.* (1970) in *Orthograptus* ? sp. and in *O. obuti* (Rickards & Koren' 1974). *Paired* apertural spines were first detected in the species by Churkin & Carter (1970) on North American specimens and confirmed by Hutt (1974) on Lake District specimens and Nicholson's type material. The actual spine bases have not been determined accurately, but on some they appear to be ventro-apertural.

Orthograptus bellulus Törnquist 1890

(Fig. 12, p. 27)

Apertural spines were noted by Törnquist (1890) in his original description, a feature which has gone unnoticed by subsequent authors until detected on the Lake District material by Hutt (1974). The Howgill Fells specimens identified as *O.* cf. *insectiformis* by Rickards (1970) should probably be referred to *O. bellulus* : pyritized specimens do not usually show the thecal spines very clearly. In the type material the spine bases are positioned ventrolaterally.

Orthograptus cyperoides (Törnquist 1897)

(Fig. 12, p. 27)

It has been noted by Hutt (1974) that *O. insectiformis* has always been identified from flattened material whereas Törnquist's (1897) species is almost always identified from specimens in relief. Two three-dimensional specimens from the Lake District were found to have very delicate thecal spines, and Hutt (1974) suggested that either they were only occasionally developed on the species, or they were rarely preserved. If the latter interpretation is correct then *O. cyperoides* may be a junior synonym of *O. insectiformis* (Nicholson 1869) which has an identical stratigraphic range and closely similar dimensions.

Genus ***RHAPHIDOGRAPTUS*** Bulman 1936

[= *Metadimorphograptus* Přibyl 1948]

Rhaphidograptus toernquisti (Elles & Wood 1906)

(Fig. 8, p. 22 ; Pl. 1, figs 1–2 ; Pl. 2, fig. 1)

The species undoubtedly possesses delicate genicular hoods (Hutt 1974), a feature which whilst probably not of great classificatory importance does at least emphasize the extremely widespread occurrence of this structure, particularly amongst Llandovery graptoloids. The thecae are usually rather loosely described as climacograptid : in fact the thecal tubes are transversely expanded, that is narrow in a dorsoventral sense, the supragenicular wall is not quite vertical, and the infragenicular wall is almost glyptograptid. The species probably reflects the acquisition of near-climacograptid features by a glyptograptid ancestor such as *G. persculptus* s.l. (Fig. 8).

Genus ***DIMORPHOGRAPTUS*** Lapworth 1876

[= *Bulmanograptus* Přibyl 1948]

Dimorphograptus sp.

(Fig. 10, p. 23)

The thecae exhibited by this species, although not yet fully understood, clearly demonstrate what has long been felt about *Dimorphograptus* species, namely that the thecal tube is not of simple orthograptid or dichograptid type. The free ventral wall of this form undoubtedly turns inward a little and the apertural margin appears to be slightly undulating. Other dimorphograptid species, such as those with 'isolated' thecae, may eventually be shown to have aberrant apertural margins.

Genus ***ATAVOGRAPTUS*** Rickards 1974

(Fig. 17, p. 37)

Generic diagnosis. Long slender rhabdosomes with gentle dorsal or flexuous curvature ; thecae glyptograptid, elongate glyptograptid, or proto-monoclimacid ; geniculation increases in later species ; sicula short in earlier forms becoming longer (up to 3 mm) in later species ; two species biform with elongate glyptograptid thecae distally and proto-monoclimacid thecae proximally.

Occurrence. *Persculptus* to *magnus* Zones.

Type species. *Atavograptus atavus* (Jones 1909) ; Pl. 4, fig. 4 ; Pl. 6, fig. 1.

Species. *A. atavus* (Jones), *A. ceryx* (Rickards & Hutt), *A. strachani* (Hutt & Rickards), *A. praestrachani* sp. nov., *A. gracilis* (Hutt), *A. renaudi* (Philipot).

Atavograptus praestrachani sp. nov.

(Fig. 17, p. 37)

1970 *Monograptus* sp. 1 ; Hutt & Rickards : 75 ; figs 3c, d.

Holotype. The specimen figured Hutt & Rickards (1970 : fig. 3c), specimen number A 60415 (Sedgwick Museum) from Keisley (National Grid ref. NY 71382379).

Diagnosis. Rhabdosome dorsally curved with a proximal dorsoventral width of 0·25 mm (low relief) increasing to 0·90 mm distally; proximal thecal spacing 9–10 in 10 mm and distally down to 7 in 10 mm; proximal thecae *strachani*-like with sharp geniculum, distal thecae *atavus*-like, flowing geniculum and apertures slightly everted; change from proximal to distal type gradual; sicula 3 mm long reaching to just above the level of the aperture of th1.

Remarks. Nothing further is added to the observations of Hutt & Rickards (1970), but the form's evolutionary position is now considered sufficiently well documented to justify its erection as a new species: morphologically and stratigraphically it is exactly intermediate between *A. atavus* and *A. strachani*.

Genus ***PRIBYLOGRAPTUS*** Obut & Sobolevskaya 1966, emend. Rickards (in press)

Emended diagnosis. Rhabdosome usually long and slender with flexuous curvature, but in one species more robust and straight, and in one with stiff curvature proximally. Sicula known in only one species where it is small reaching to about the aperture of th1. Thecae long, slender, usually inclined at less than 20 degrees to the axis of the rhabdosome, and with *pronounced* introversion of the apertural region which may also be furnished with a pair of lateral horns directed dorsolaterally, and overhung by a geniculum and perhaps with a genicular hood.

Type species. *Monograptus incommodus* Törnquist 1899.

Genus ***CORONOGRAPTUS*** Obut & Sobolevskaya (*in* Obut *et al.*) 1968, emend. Rickards (in press)

Emended diagnosis. Rhabdosomes mostly quite short, up to 40 mm, relatively robust with dorsal curvature varying from stiff to horseshoe-shaped. Sicula in early forms about 2 mm, but up to 12 mm in later species. Thecae relatively long, usually overlapping at least half the ventral wall, with a *rounded* geniculum pronounced in some species; thecal apertures even or slightly everted, and rarely isolate growing out over the geniculum and obscuring it.

Type species. *Monograptus gregarius* Lapworth 1876.

Remarks. In addition to the species discussed above, p. 41, *M. leei* Hsü and *M.* sp. Hutt (1975) should probably also be included here: the latter shows some features intermediate between *Atavograptus* and *Coronograptus*.

Genus ***LAGAROGRAPTUS*** Obut & Sobolevskaya (*in* Obut *et al.*) 1968, emend. Rickards (in press)

Emended diagnosis. Rhabdosome with moderate dorsal curvature, relatively slim and parallel-sided. Sicula long but reaching at most to just above the aperture of th1; sicular aperture asymmetrical as in *C. gregarius*. Thecae long, slender, overlapping half to more than three-quarters of ventral wall; thecal apertures slightly everted, with semicircular excavation and pronounced overhanging geniculum which may have genicular hood; striking *ventral apertural* process of triangular shape composed of fusellar tissue.

TYPE SPECIES. *Lagarograptus inexpeditus* Obut & Sobolevskaya (*in* Obut *et al.*) 1968.

REMARKS. The fusellar structure of the ventral apertural process has recently been established by one of us (R. B. R.) on Saudi Arabian specimens referable to *L.* cf. *tenuis* (Portlock), and there is a suggestion of fusellar growth bands on the type specimens from Norilsk. The genicular hood may possibly also be composed of fusellar tissue.

Genus ***MONOGRAPTUS*** Geinitz 1852, emend.

Monograptus sudburiae Hutt 1974

(Figs 17, p. 37, and 19, p. 43)

1958 *Monograptus revolutus* C; Sudbury: 536, textfig. 26c.

Hutt's (1974) species is the type of a newly-defined group of biform monograptids in which the proximal thecae display retroverted hooks and the distal thecae strong introversion. The change is gradual throughout the rhabdosome. The most proximal thecae have a dorsoventral width of less than 0·20 mm, and a thecal spacing of 7½ in 10 mm, and no thecal overlap; distally the dorsoventral width is 0·50–0·60 mm (in relief), the thecal spacing 10–10½ in 10 mm and the thecal overlap about a half. Just before the maximum thecal overlap develops, coinciding with a tightening of the rhabdosome's curvature, the thecae become introverted. *M. revolutus* Kurck 1882 displays the same basic structure but has a more robust rhabdosome and a more restricted occurrence (*cyphus* Zone).

Monograptus delicatulus Elles & Wood 1913

(Fig. 38, p. 73)

Material from the Soviet Union recently isolated seems to fit Elles & Wood's (1913) description very well but in addition displays very long, slender, ventro-laterally-directed spines. The thickened dorsal lip of the hook depends proximally between the spines, which may have evolved from an original paired horn structure. The sicula of the Russian specimens has a pronounced curvature.

Monograptus walkerae nom. nov.

1958 *Monograptus toernquisti* sp. nov.; Sudbury: 514.

Stein (1965) has pointed out that Sudbury's (1958) species name is a junior homonym of *M. toernquisti* (Eisel 1912), and we herein propose the new name *M. walkerae* to replace *M. toernquisti, sensu* Sudbury (née Walker). Similarly *M. toernquisti elongatus* Sudbury is a junior homonym of *M. elongatus* Törnquist 1899, and we herein propose the name *M. walkerae rheidolensis* as a new name for Sudbury's subspecies.

Monograptus sp. A

(Fig. 25, p. 56)

The single specimen from the *gregarius* Zone of Dobb's Linn, probably *magnus* level, was collected by Dr H. Jaeger on the 1969 Ludlow Research Group excursion, and is the earliest known *Monograptus* s.s. The length of the rhabdosome is 67 mm and displays conspicuous gentle dorsal curvature throughout: the dorsoventral width (almost flattened) is 0·4–0·5 mm at the level of th1 and th2, 0·7–0·8 at th20–24, and distally achieves 0·90 mm. The sicula has a length of about 1·3 mm, its apex reaching to the top of th1. Thecal spacing at the proximal end is 10 in 10 mm falling to 9–10 in 10 mm more distally. Thecal overlap is not clear but probably small. The thecae are uniform except that the distal thecal hooks exhibit dorsal wall retroversion to the extent that the hook looks almost spinose (Fig. 25, p. 56). The ventral wall of the theca seems not to participate in the hook, which is therefore best described as a very pronounced hood. Although growth lines are difficult to discern they have been detected on the hood of th60, for example, and a few other thecae, indicating that the hood is composed of fusellar tissue. *M.* cf. *concinnus* occurs on the same slab as *M.* sp. A, and Toghill records *M. concinnus* from the top of the *gregarius* Zone in Dobb's Linn.

Monograptus turriculatus Barrande 1850

(Fig. 36, p. 71)

Hutt (1975) has recently recorded bifurcating apertural spines in this species, thus supporting the preliminary observations of Bulman & Rickards (*in* Bulman 1970), although it should be emphasized that the actual detailed structure of the thecae is not yet known. We support earlier suggestions that in Britain, at least, *M. turriculatus minor* Bouček cannot be distinguished. Mr L. Sherwin has informed us of a species superficially similar to *M. turriculatus* from the Cotton Beds of the Forbes District in Australia, which differs from the latter mainly in having a shorter sicula and a lower conical spiral so that specimens are most commonly preserved on the bedding plane in the form of a plane spiral.

Genus ***PRISTIOGRAPTUS*** Jaekel 1889

Pristiograptus spp. 1 and 2

(Figs 30, p. 65, and 55)

Two unnamed species have been described by Hutt (1974) from the *magnus* and *argenteus* Zones of the Lake District, sp. 1 occurring only in the *magnus* Zone, and sp. 2 in both zones. *P.* sp. 1 has a sicula 1·3–1·4 mm long, a thecal spacing of 10 in 10 mm proximally and 11½ in 10 mm distally, and a dorsoventral width of 0·20 mm at the level of th1 increasing to 0·5 mm at th9 (flattened). The thecal apertures are horizontal, even fractionally introverted, and the appearance as a whole is of a form intermediate between *A. atavus* and later pristiograptids.

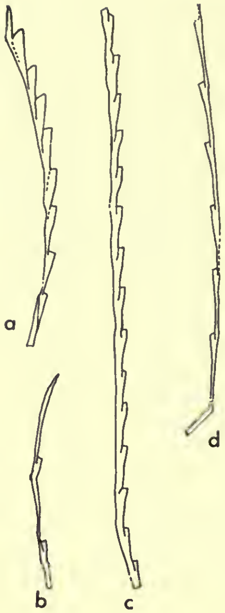


Fig. 55. Early pristiograptids: a, *P.* sp., LU 57771, *magnus* Zone, Skelgill, Lake District; b, *P. fragilis* (Rickards), LU 57589, *acinaces* Zone, Yewdale Beck, Lake District; c, *P.* sp., LU 57772, *magnus* Zone, Skelgill, Lake District; d, *P. fragilis* (Rickards), LU 57587, *magnus* Zone, Yewdale Beck, Lake District. All figures × 5.

The proximal end of *P.* sp. 2 is not known but the fragments have a dorsoventral width of 0·30–0·35 mm and a thecal spacing of 10 in 10 mm. Overlap is one-eighth and the angle of inclination a little over 10 degrees.

VIII. IN RETROSPECT

A general survey of the main features in the evolution of Siluro-Devonian graptoloids is indicated in Fig. 1, p. 7. To be noted is the rapid diversification of the Silurian graptolites into many lineages during the early and middle Llandovery following an interval near the end of the Ordovician during which so many lineages of graptolites died out that they came close to becoming totally extinct. Early Silurian diversification appears to have reached its peak in about the *cyphus* Zone. Relatively gradual reductions took place in most lineages throughout the remainder of the Llandovery, a trend which culminated in the extinction or near-extinction of many graptolite stocks in the latest Llandovery–early Wenlock interval. At that time, the genera *Averianowograptus*, *Barrandeograptus*, *Damosiograptus*, *Diversograptus*, *Oktavites*, *Spirograptus*, *Streptograptus*, *Uralograptus* and the retiolitids (*Retiolites*, *Stomatograptus*) became extinct. The stocks included herein as late Llandovery 'cyrtograptids' became extinct or nearly so during the *riccartonensis* Zone. They were replaced in strata above the *riccartonensis* Zone by one or more new 'cyrtograptid' lineages that probably developed from ancestors other than the late Llandovery 'cyrtograptids'. In addition, the monoclimacids and monograptids s.s. were reduced in diversity in the early Wenlock.

The latest Llandovery–early Wenlock extinctions and reductions in diversity were followed during the remainder of the Wenlock by three essentially stable, widely-found stocks, the pristiograptids, the monoclimacids and the monograptids s.s. Certain short-lived stocks such as the *flexilis* group developed from the monograptids, and a number of species arose among the pristiograptids. The latter part of the Wenlock is typified by the appearance of members of the Subfamily Plectograptinae (including *Gothograptus* and *Plectograptus*) and the lineages of post-*riccartonensis* Zone 'cyrtograptids'.

A relatively sudden 'burst' in diversity or marked development of several new lineages characterizes the early Ludlow. The newly-appearing lineages probably were derived from the pristiograptid lineage. Representatives of *Bohemograptus, Colonograptus, Neodiversograptus* and *Saetograptus* as well as members of the *uncinatus* group typify the early Ludlow radiation. These and the other stocks that developed during the early Ludlow 'burst' were relatively short-lived as their numbers dwindled markedly in the latter part of the Ludlow.

At least three new stocks (the *formosus* group, the *transgrediens* group and the earliest members of the *hercynicus–yukonensis* lineage) appeared in the latest Ludlow–early Pridoli. Members of the *hercynicus–yukonensis* lineage survived into the early Devonian and probably included the youngest and last of the graptolites. The appearance of *M. uniformis* in the *hercynicus–yukonensis* lineage as well as the appearance of certain other taxa such as *Abiesgraptus* (developed from *Linograptus*) denote the base of the Devonian.

The general evolutionary history is thus one of marked radiation into many stocks in the early part of the Llandovery followed by reduction in most lineages, culminating in marked extinctions and reductions in the early Wenlock *riccartonensis* Zone. That event was followed by stability in most stocks and appearance of only a few new lineages until the early Ludlow when a relatively small but marked 'burst' in radiation occurred. Thereafter the number of graptolite stocks diminished although some replacements of those that became extinct by new stocks did take place up until the latter part of the early Devonian.

A review of the general trends in rhabdosome and thecal characteristics observed among the Siluro-Devonian graptolites indicates that many of these features appear in several different lineages. Acquisition of features such as thecal hooks and spines or spiral rhabdosome form by members of different lineages suggests that the features had an adaptive significance and were of importance not only in modes and places of life of the colonies but also in colony survival. For example, protection of the apertural region appears to have been important for colonies of many lineages. It was achieved through thecal introversion and retroversion as well as spines and probably hooks and hoods.

Analysis of evolutionary patterns among the Siluro-Devonian graptolites indicates a contrast in mode of appearance of founder species of new lineages. Some stocks, such as the rastritids, demirastritids, neodiversograptids and saetograptids, appear in the stratigraphic record relatively suddenly as morphologically clearly-defined taxa. These and similar stocks were relatively short-lived, in general. In contrast with them, the original or founding species of long-lived stocks such as the pristiograptids, monoclimacids and monograptids are not clearly distinguishable. In the case of such stocks, the species that are possible candidates as their initial members are closely similar morphologically to species in the lineage from which they originated. This relationship is consistent with the processes of speciation described by Mayr (1963), among others, in which new species are visualized as developing as local populations from a parental population or group of local populations by some form of isolation. In the speciation process as discussed by Mayr, a newly-developed daughter species may be little different morphologically from its parent and yet, when the phyletic history of whole lineages is established, such a daughter may be recognized as the initial member of a new lineage. The available record of the origin of some Siluro-Devonian graptolite lineages, such as the pristiograptids and monoclimacids, appears to be at least consistent with if not fully corroborative of such a theoretical pattern of speciation leading to the origin of a new lineage.

The contrasting patterns in evolutionary development may reflect differences in the availability of potential niches for graptolite species, particularly those with new modes or places of life. The lineages that arose with founder species showing little morphological difference from their parental species appeared at times when many different lineages were in existence and probably potential niches were fully or almost fully exploited. The lineages in which the initial members appear in the stratigraphic record as new taxa, relatively clearly morphologically different, developed at times when few lineages were present. Many potential niches appear to have been available at times when few lineages were in existence. The widespread availability of potential niches appears, from the evolutionary history of the Siluro-Devonian graptolites, to have been a major factor in the marked adaptive radiations or 'bursts' in taxonomic diversity.

Although certain aspects of the evolutionary history suggested herein may, and probably will, be modified through future researches, the basic patterns appear to be relatively well founded. Initial versions of Fig. 1 (p. 7) were developed in 1966–67. They have been tested through vigorous and detailed stratigraphic collecting by the authors over seven years in different areas in the world. In addition, existing collections from many parts of the Siluro–Devonian succession in several areas of the world have been examined. These critical studies have not substantially modified most of the basic aspects of the initially-recognized lineages and their relationships, although many new details have been discovered and used to refine the initial versions of Fig. 1 and produce the version herein. Future work will doubtless pinpoint phyletic intermediates along some lineages and suggest range extensions and expansions of others. Despite these expected and, indeed, hoped-for modifications, the basic patterns indicated provide a tool that stratigraphers interested in dating Silurian–early Devonian rocks using graptolites may use. The phyletic developments indicated in Fig. 1 may also be used to refine understanding of the zonal sequence because the appearance of a new lineage is a unique event which may be considered an appropriate marker of a zone boundary, or at least a point in time.

Evolutionary development as indicated in Fig. 1 and discussed in the text may be analysed from different points of view, which include, in addition to increasing comprehension of the patterns of organic evolution, the establishing of possible relationships between adaptive radiation and availability of potential niches, making age determinations, and refining zone boundaries.

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New taxonomic names and the page numbers of the principal references are printed in **bold** type. An asterisk (*) denotes a figure.

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PLATE 1

Rhaphidograptus toernquisti (Elles & Wood) (pp. 23, 102; see also Pl. 2, fig. 1)

FIG. 1. Q 5011. Skelgill Beds, *cyphus* Zone, Llandovery ; Mealy Gill, Lake District. × 10.
FIG. 2. Q 5012. As last. × 10.

Dimorphograptus elongatus Lapworth (p. 23)

FIG. 3. Q 5013. Skelgill Beds, *atavus* Zone, Llandovery ; School Beck, Lake District. × 5.

Diplograptus modestus modestus Lapworth (p. 16)

FIG. 4. Q 5014. Skelgill Beds, Llandovery ; Yewdale Beck, Lake District. × 10.

Climacograptus medius Törnquist (p. 18)

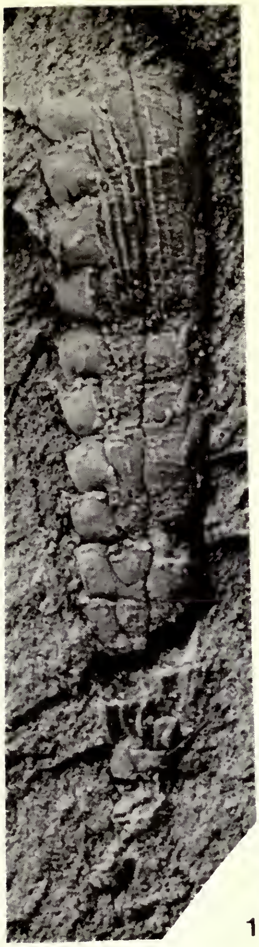
FIG. 5. Q 5015. *Acinaces* Zone, Llandovery ; Clywedog Gorge, Montgomery, Powys, Wales. × 10.

Diplograptus cf. ***diminutus*** Elles & Wood (p. 16)

FIG. 6. Q 5016. *Persculptus* Zone, Llandovery ; Yewdale Beck, Lake District. × 10.

Orthograptus truncatus Lapworth (p. 25)

FIG. 7. Q 5017. Hartfell Shales, Ordovician ; Dobb's Linn, Moffat, Scotland. × 10.



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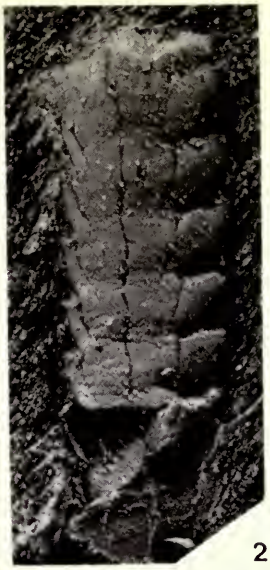

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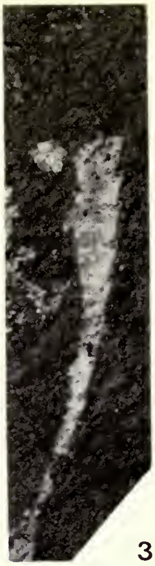

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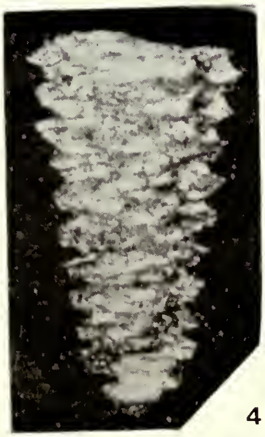

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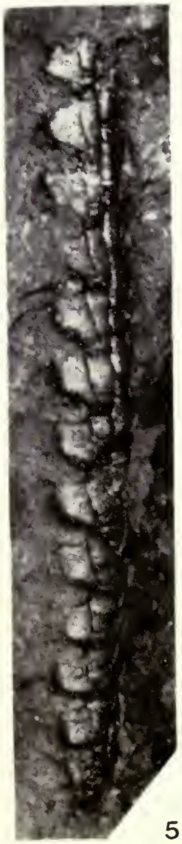

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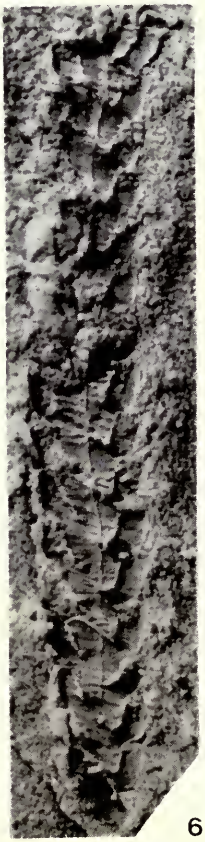

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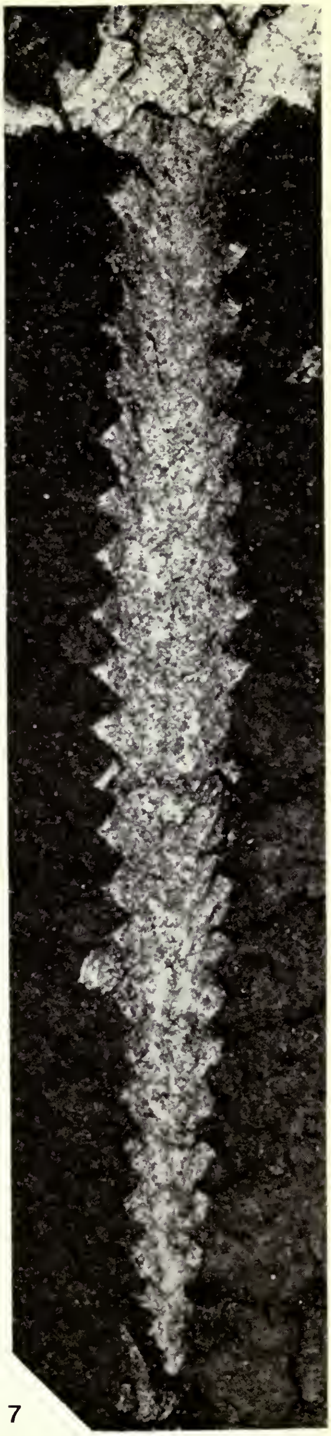

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PLATE 2

Rhaphidograptus toernquisti (Elles & Wood) (pp. 23, 102; see also Pl. 1, figs 1–2)

FIG. 1. Q 5018. Skelgill Beds, *atavus* Zone, Llandovery; Yewdale Beck, Lake District. × 10. Climacograptid aspect.

Petalograptus cf. ***minor*** Elles (p. 29),
Pseudoclimacograptus (Metaclimacograptus) hughesi (Nicholson) (p. 14) and
Monograptus triangulatus cf. ***separatus*** Sudbury (p. 46).

FIG. 2. Q 5019a–c. Skelgill Beds, *magnus* Zone, Llandovery; Skelgill, Lake District. × 10.

Orthograptus acuminatus (Nicholson) (p. 28), and
fragments of ***Climacograptus normalis*** Lapworth (p. 17; see also Pl. 3, fig. 4)

FIG. 3. Q 5020a–b. Birkhill Shales, *acuminatus* Zone, Llandovery; Main Cliff, Dobb's Linn, Moffat, Scotland. × 5.

Glyptograptus persculptus (Salter) (pp. 20, 99)

FIG. 4. Q 5021. *Persculptus* Zone, Llandovery; R. Severn, Montgomery, Powys, Wales. × 2½.

Pristiograptus nudus (Lapworth) (p. 64)

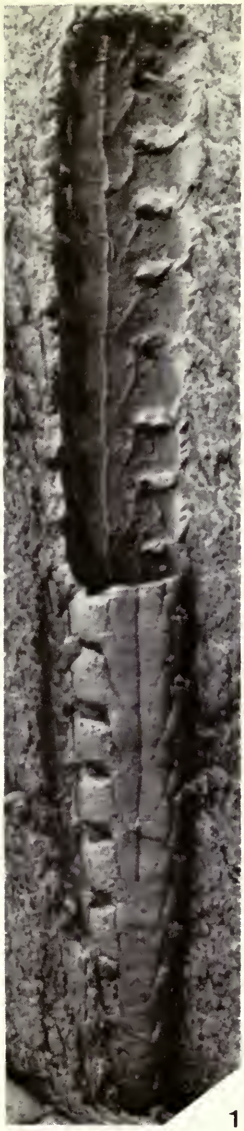
FIG. 5. Q 5022. Browgill Beds, *crispus* Zone, Llandovery; Stockdale Beck, Lake District. × 10. On same slab as Fig. 6.

Monograptus exiguus Nicholson (p. 73)

FIG. 6. Q 5023. × 10. Same locality and on same slab as Fig. 5.

Cystograptus vesiculosus (Nicholson) (p. 25)

FIG. 7. Q 5024. Skelgill Beds, *atavus* Zone, Llandovery; Yewdale Beck, Lake District. × 10. Sicula and first few thecae.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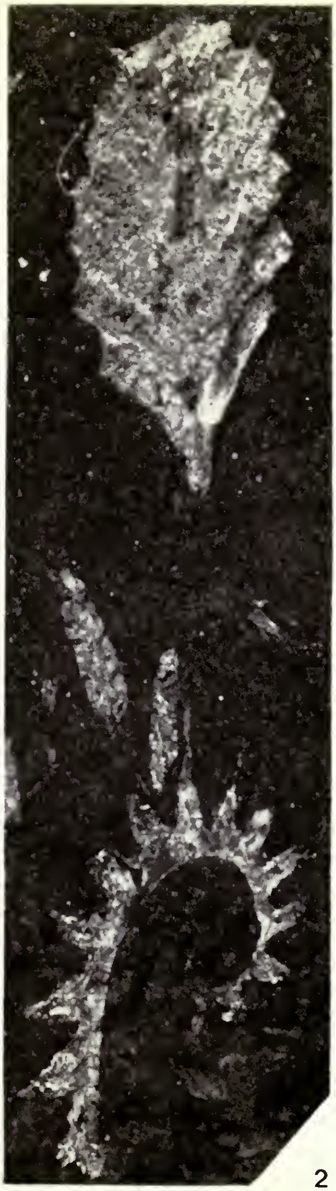
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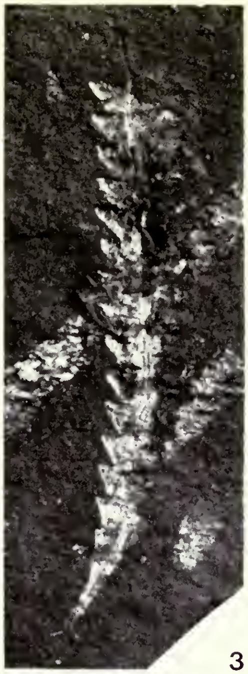
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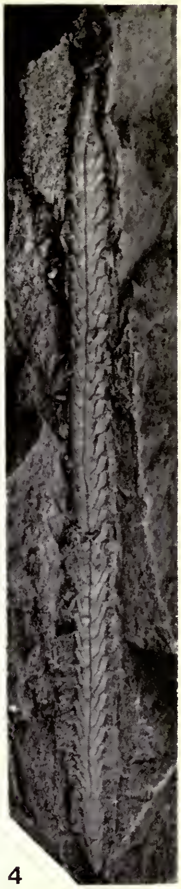
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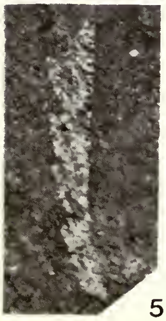
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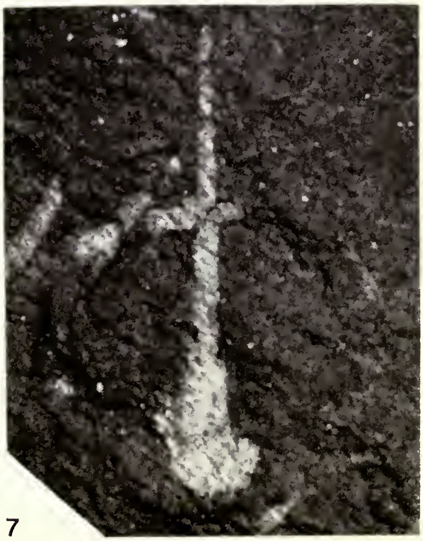
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PLATE 3

Diplograptus magnus H. Lapworth (p. 16)

FIG. 1. Q 5025. *Magnus* Zone, Llandovery ; Clywedog Gorge, Montgomery, Powys, Wales. × 10.

FIG. 5. Q 5029. *Magnus* Zone, Llandovery ; stream south of Blackman's Hall, Van Mines, Montgomery, Powys, Wales. × 10. Specimens showing varied preservation and deformation.

Petalograptus sp. (p. 29)

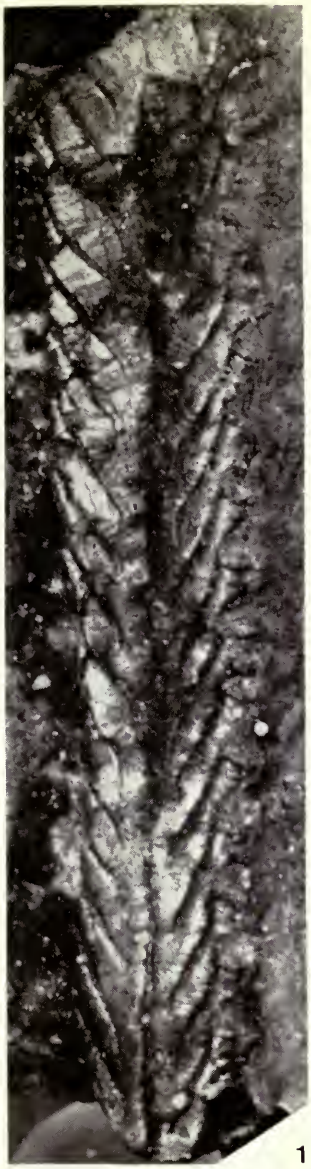
FIG. 2. Q 5026. *Cometa* horizon, *convolutus* Zone, Llandovery ; Dobb's Linn, Moffat, Scotland. × 10.

Monograptus discus Törnquist (p. 87)

FIG. 3. Q 5027. Skelgill Beds, *crispus* Zone, Llandovery ; Stockdale Beck, Lake District. × 10.

Climacograptus normalis Lapworth (p. 17 ; see also Pl. 2, fig. 3)

FIG. 4. Q 5028. Skelgill Beds, *acuminatus* Zone, Llandovery ; Yewdale Beck, Lake District. × 10. Specimen deformed, lineation at right angles to length of rhabdosome.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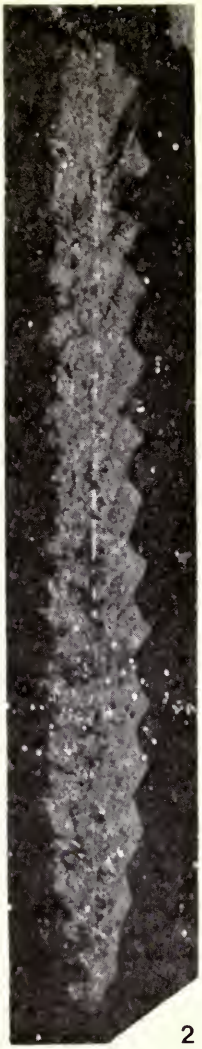
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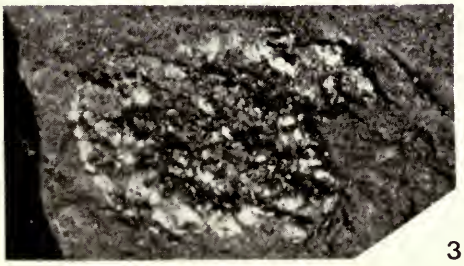
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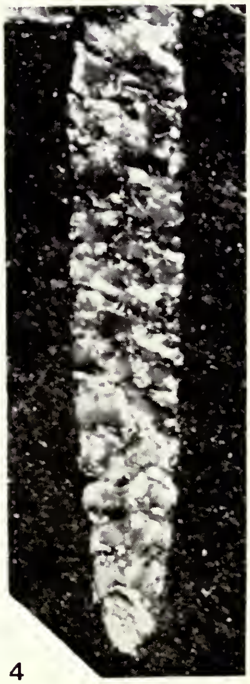
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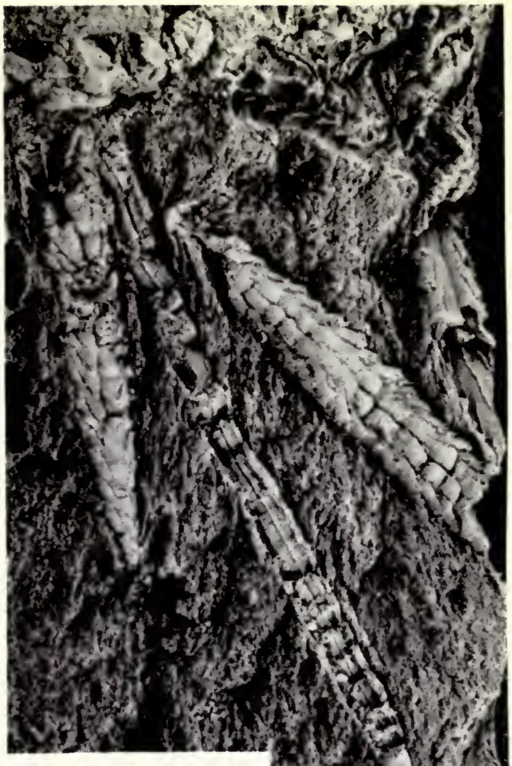
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PLATE 4

cf. **Diplograptus magnus** H. Lapworth (p. 16)

FIG. 1. Q 5030. *Magnus* Zone, Llandovery ; stream south of Blackman's Hall, Van Mines, Montgomery, Powys, Wales. × 10. Reverse view.

FIG. 2. Q 5031. As last. × 10.

Monograptus clingani (Carruthers) (p. 52)

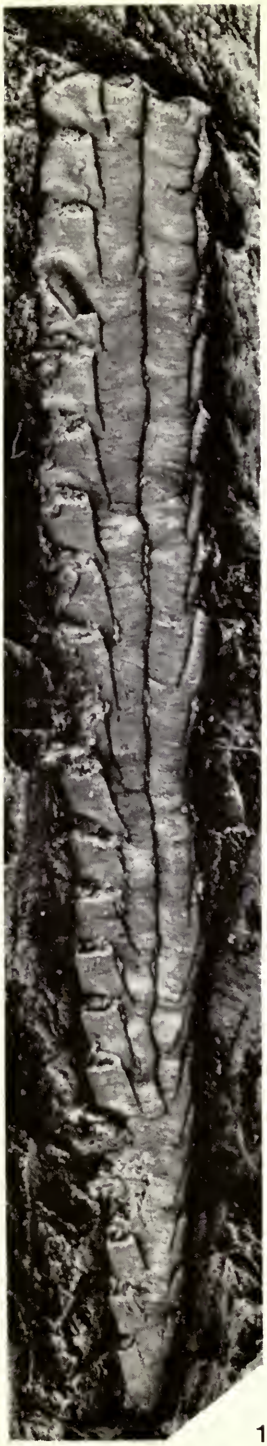
FIG. 3. Q 5032. Birkhill Shales, Llandovery ; Dobb's Linn, Moffat, Scotland. × 10.

Atavograptus atavus (Jones) (pp. 38–40 ; see also Pl. 6, fig. 1)

FIG. 4. Q 5033. Skelgill Beds, *cyphus* Zone, Llandovery ; Mealy Gill, Lake District. × 5.

Atavograptus sp. [= *Monograptus* sp. 2 of Hutt & Rickards 1970 : 76] (p. 39)

FIG. 5. Q 5034. Skelgill Beds, *atavus* Zone, Llandovery ; School Beck, Lake District. × 1. Hundreds of current-sorted rhabdosomes ; at the top of the illustration the actual thickness of piled and flattened rhabdosomes is 3 mm.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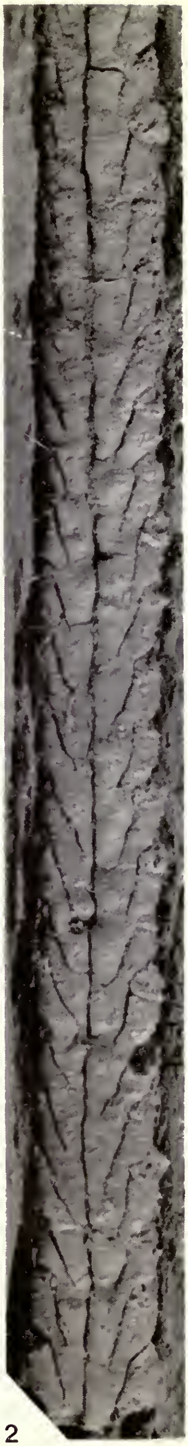
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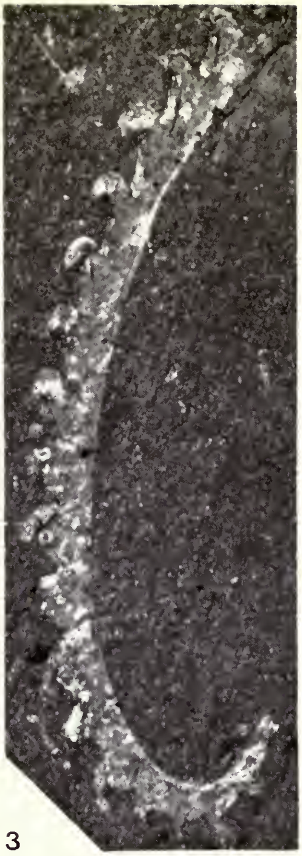
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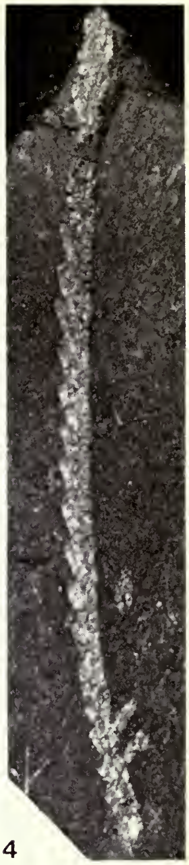
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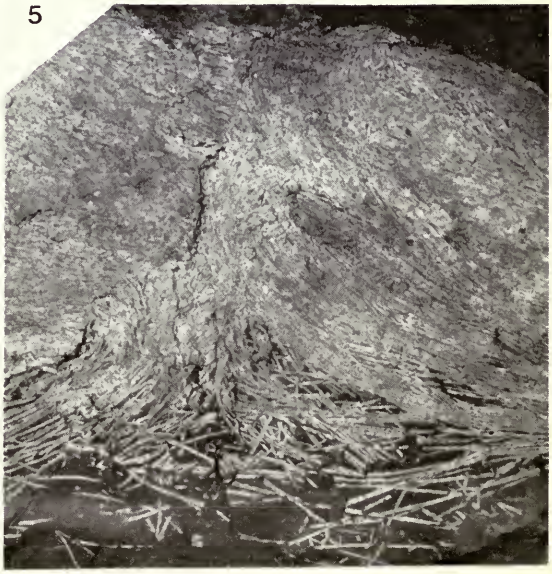


PLATE 5

Monograptus convolutus (Hisinger) (p. 46)

Fig. 1. Q 5035. *Cometa* horizon, *convolutus* Zone, Llandovery ; Clywedog Gorge, Montgomery, Powys, Wales. × 10.

Monograptus triangulatus cf. **_major_** Elles & Wood (p. 46)

Fig. 2. Q 5036. *Leptotheca* Zone, Llandovery ; south-east of Pwll-gwinau, Nant yr Hebog, Montgomery, Powys, Wales. × 5.

Monograptus triangulatus triangulatus (Harkness) (p. 46)

Fig. 3. Q 5037. '*Gregarius*' Zone, Llandovery ; Dobb's Linn, Moffat, Scotland. × 10.

Monograptus lobiferus M'Coy (p. 58)

Fig. 4. Q 5038. *Convolutus* Zone, Llandovery ; Bron Felin, near Old Hall, R. Severn, Montgomery, Powys, Wales. × 5.

Monograptus sedgwickii (Portlock) (p. 48)

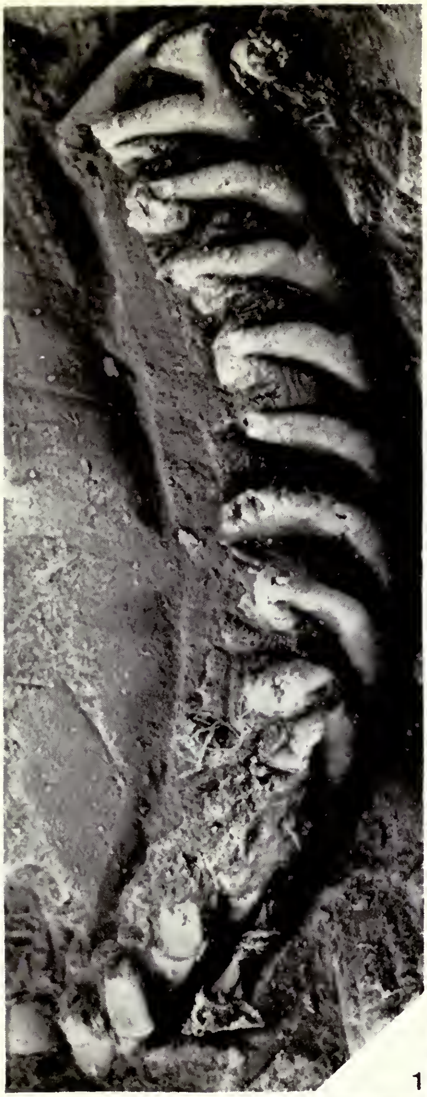
Fig. 5. Q 5039. *Sedgwickii* Zone, Llandovery ; Church Beck, Lake District. × 5.

Monograptus triangulatus fimbriatus (Nicholson) (p. 46)

Fig. 6. Q 5040. Skelgill Beds, *magnus* Zone, Llandovery ; Skelgill, Lake District. × 10.

Pristiograptus regularis Törnquist (p. 64)

Fig. 7. Q 5041. *Convolutus* Zone, Llandovery ; Bron Felin, near Old Hall, R. Severn, Montgomery, Powys, Wales. × 5.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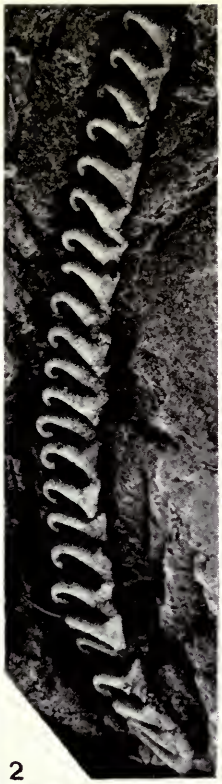
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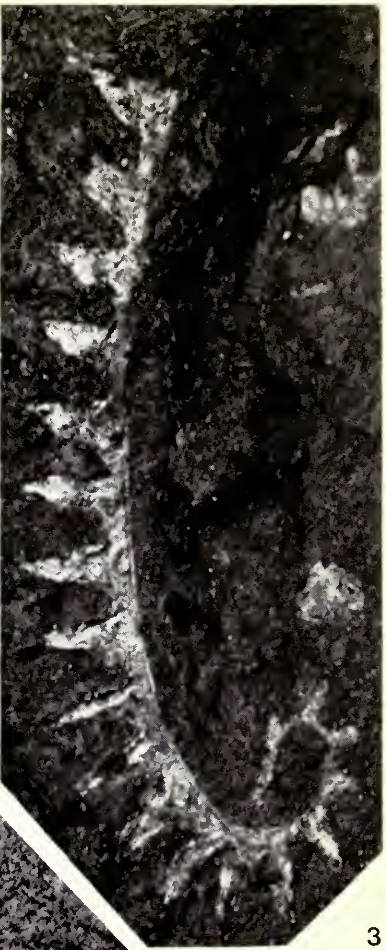
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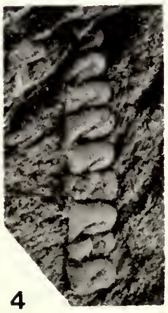
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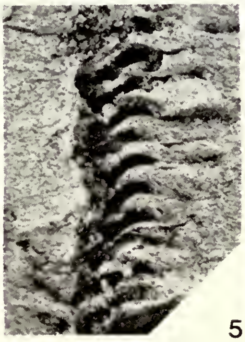
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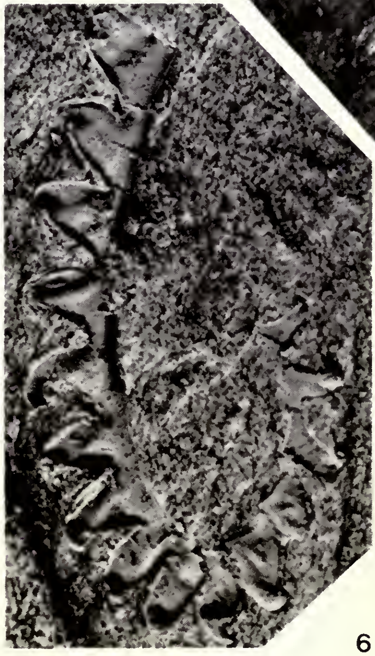
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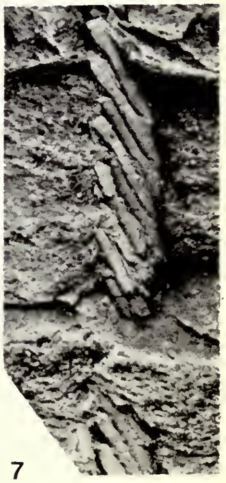
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PLATE 6

Atavograptus atavus (Jones) (pp. 38–40 ; see also Pl. 4, fig. 4)

FIG. 1. Q 5042. Skelgill Beds, *cyphus* Zone, Llandovery ; Yewdale Beck, Lake District. × 5. Distal thecae in relief.

Monograptus marri (Perner) (pp. 48, 60)

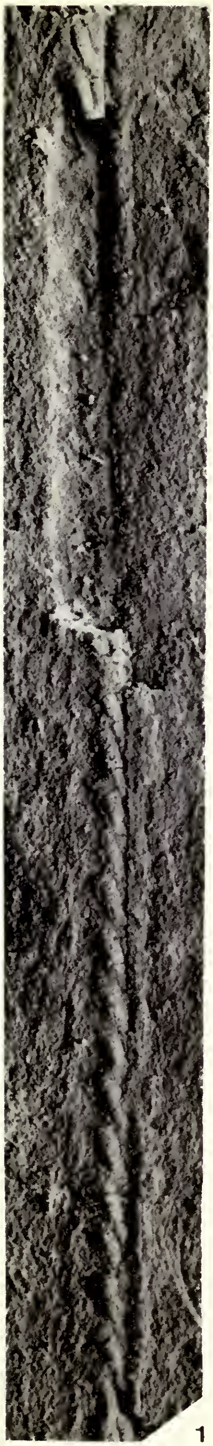
FIG. 2. Q 5043. Browgill Beds, *crispus* Zone, Llandovery ; Stockdale Beck, Lake District. × 10. Distal thecae, lineation showing direction of elongation at right angles to rhabdosome length.

Lagarograptus acinaces (Törnquist) (p. 42)

FIG. 3. Q 5044. *Acinaces* Zone, Llandovery ; Blackman's Hall, Van Mines, Montgomery, Powys, Wales. × 5. Specimen lacking preserved ventral apertural processes.

Monoclimacis crenulata *sensu* Elles & Wood (p. 54)

FIG. 4. Q 5045. *Crenulata* Zone, Llandovery ; Tach Wood, Glyn Brook, Montgomery, Powys, Wales. × 5. Showing thecal eversion and thecal processes.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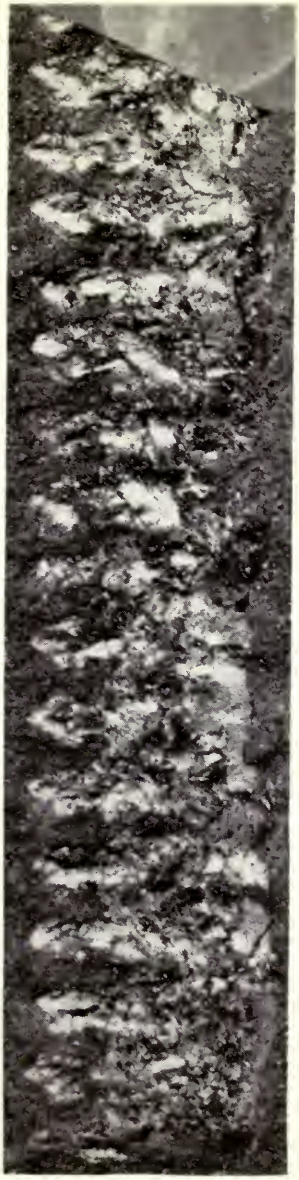
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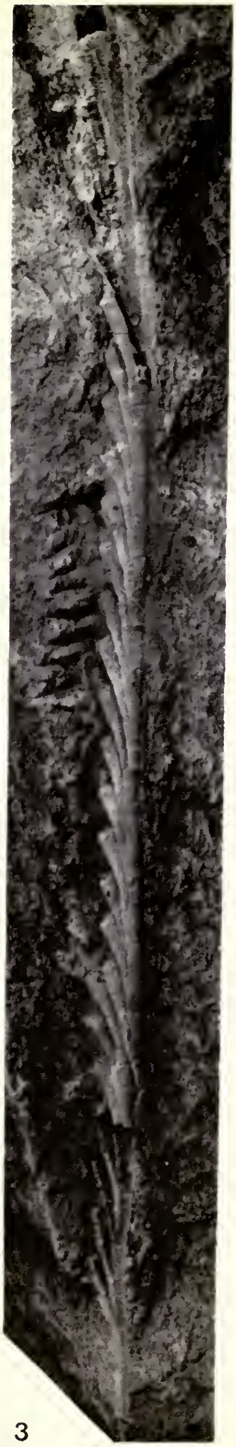
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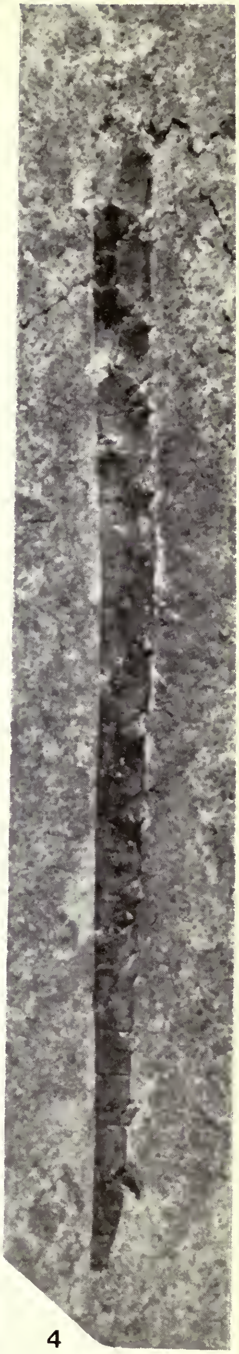
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THE OSTEOLOGY OF *NOTELOPS* WOODWARD, *RHACOLEPIS* AGASSIZ AND *PACHYRHIZODUS* DIXON (PISCES : TELEOSTEI)

P. L. FOREY

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
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THE OSTEOLOGY OF *NOTELOPS* WOODWARD, *RHACOLEPIS* AGASSIZ AND *PACHYRHIZODUS* DIXON (PISCES : TELEOSTEI)

BY

PETER L. FOREY

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Pp. 123–204 ; 39 *Text-figures*

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THE OSTEOLOGY OF *NOTELOPS* WOODWARD, *RHACOLEPIS* AGASSIZ AND *PACHYRHIZODUS* DIXON (PISCES: TELEOSTEI)

By PETER L. FOREY

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SYNOPSIS

The osteology of representative species of the Cretaceous teleosts *Notelops* Woodward, *Rhacolepis* Agassiz and the English species of *Pachyrhizodus* Dixon is described. *Thrissopater* Günther is placed in synonymy with the genus *Pachyrhizodus*. *Notelops, Rhacolepis* and *Pachyrhizodus* are considered to form a monophyletic group based on the common possession of patterns of derived character states in the circumorbital series and the caudal skeleton. The suborder Pachyrhizodontoidei is erected to contain these genera. The complement of derived character states shown by the pachyrhizodontoids is comparable with that shown by protacanthopterygian euteleosts, in particular with the salmonoids. However, as neither the Euteleostei nor the Protacanthopterygii can, as yet, be defined, the Pachyrhizodontoidei are left as Teleostei *incertae sedis*. *Rhacolepis* and *Pachyrhizodus* are grouped together in the family Pachyrhizodontidae Cope. *Notelops* is placed in a new family Notelopidae and stands as the plesiomorph sister-group of the Pachyrhizodontidae.

I. INTRODUCTION

THIS PAPER is concerned with the osteology of the Cretaceous teleosts *Notelops* Woodward, *Rhacolepis* Agassiz, *Thrissopater* Günther and *Pachyrhizodus* Dixon. A few notes are added concerning the lesser known genus *Elopopsis* Heckel. At the time of writing Ms S. Teller, of the Department of Biology, University of Illinois at Chicago Circle, is undertaking a review of the North American species of *Pachyrhizodus* and consequently only the English species of *Thrissopater* and *Pachyrhizodus* are treated in detail in the present paper. The work arises from a broader study on the fishes included by Woodward (1901) in the families Elopidae and Albulidae. Part of the results have been published (Forey 1973a, b) and revisions of *Spaniodon* and *Thrissopteroides* will be published elsewhere.

The genera to be dealt with here were included by Woodward (1901) in the family Elopidae. Within the Elopidae Woodward (1901 : 7–8) recognized, in the form of a key, two groups of genera. One of these groups, later termed the 'elopine group' by Dunkle (1940), is characterized by showing medially united parietals and includes *Notelops* and *Elopopsis* of the fishes to be dealt with here. The other group, the 'spaniodontine group' of Dunkle (1940), shows separated parietals and includes *Rhacolepis*, *Thrissopater* and *Pachyrhizodus*. This separation of *Notelops* from *Rhacolepis*, *Thrissopater* and *Pachyrhizodus* appears to have been followed by most subsequent workers, some of whom have placed the latter genera in a separate family or families.

Notelops Woodward and *Rhacolepis* Agassiz are known only from the Santana Formation of the Araripe plateau, Ceará, Brazil. This formation is reputed to be Aptian in age and to represent an estuarine deposit (Santos & Valença 1968; Mabesoone & Tinoco 1973). The anatomy of *Notelops* was briefly described by Woodward (1887, 1901), Jordan (1907, 1921) and Jordan & Branner (1908). Dunkle (1940) described, in great detail, the cranial osteology of *Notelops*, his description being based on the serial sectioning of a single specimen. I have been able to check this description against several acid-prepared specimens and have added information; the postcranial skeleton has never been examined in detail hitherto. *Notelops* has always been placed in the family Elopidae with the recognition that it is closely related to *Elops*. Thus Dunkle (1940 : 187) wrote: '*Elops* can be regarded as an unmodified descendant of a form closely related to *Notelops*'. To date, this statement remains unchallenged.

Elopopsis Heckel is a genus known by several species from the Cenomanian of Jugoslavia, Czechoslovakia, Morocco, the Turonian of England and the Campanian of Westphalia. None of the species is particularly well known. *Elopopsis* was first classified (Woodward 1901) as an 'elopine elopid' but the probable separation of the parietals (Woodward 1908) should have placed it in the 'spaniodontine group'. Applegate (1970) places *Elopopsis* in association with *Thrissopater, Pachyrhizodus* and *Rhacolepis* in the superfamily Pachyrhizodontoidae, comprising the single family Pachyrhizodontidae Cope.

Brief descriptions of *Rhacolepis* have been given by Woodward (1887, 1901), Jordan (1921) and Jordan & Branner (1908). The availability of several specimens that could be prepared in acid has resulted in an almost complete description of the osteology. *Rhacolepis* was placed in the Elopidae by Woodward (1901) although both that author and several others (Dunkle 1940, Applegate 1970 and Santos & Valenca 1968) have recognized that it is morphologically more similar to *Thrissopater* and *Pachyrhizodus* than to *Notelops*.

Thrissopater Günther is represented by two species from the Cretaceous of England, *T. salmoneus* Günther from the Albian and *T. megalops* Woodward from the Cenomanian. Each of these species is known by only a handful of specimens. I can add little to the descriptions of *T. salmoneus* given by Günther (1872) and Woodward (1901). A specimen of *T. megalops* was prepared in acetic acid and used as the basis for a detailed description of the cranium. During the course of this work it became apparent that there were no significant differences between the genera *Thrissopater* and *Pachyrhizodus* and it is suggested that *Thrissopater* be included within the genus *Pachyrhizodus*. However *Thrissopater daguini* Arambourg (1954), from the Cenomanian of Morocco, shows little resemblance to other species of *Thrissopater*.

Thrissopater has been considered as a 'spaniodontine elopid' by Woodward (1901) and Dunkle (1940). Jordan (1905) included *Thrissopater* with *Spaniodon* in the family Spaniodontidae, a family which was thought to be closely related to the Elopidae. Boulenger (1910) placed *Thrissopater* as a monogeneric subfamily, the Thrissopatrinae, in the family Clupeidae, stating that this genus is a link between the Elopidae and the Clupeidae. Bertin & Arambourg (1958 : 2214) recognized *Thrissopater* as very similar to *Pachyrhizodus* and placed both in the family Thrissopateridae. The Thrissopateridae were placed in the suborder Elopoidei together with the Elopidae, Albulidae and Pterothrissidae.

Pachyrhizodus Dixon is known from marine Cretaceous deposits of England, North America and Australia. The English species, represented mostly by cranial fragments, have been excellently described by Woodward (1901, 1907, 1908, 1911). The North American species have received attention in works by Stewart (1898, 1899), Loomis (1900), Hay (1903), Cope (1874, 1875) and Applegate (1970). *Pachyrhizodus marathonensis* (Etheridge) from Australia is most completely described by Bartholomai (1969).

Pachyrhizodus is the type genus of the family Pachyrhizodontidae Cope. Cope (1872) included within the family other genera that are probably synonymous with *Pachyrhizodus*, and placed the Pachyrhizodontidae in association with the Saurodontidae and the Ichthyodectidae. Later Cope (1875) abandoned the Pachyrhizodontidae and placed *Pachyrhizodus* with *Stratodus* Cope and *Cimolichthys* Leidy in the family Stratodontidae. Fowler (1911) erected the family Raphiosauridae, based on the mistaken assumption that *Raphiosaurus* was the senior synonym of *Pachyrhizodus*. Jordan (1923) maintained the Raphiosauridae (= Pachyrhizodontidae) to include eleven genera, nine of which are junior synonyms of *Pachyrhizodus*, while the remaining genus, *Anogmius* Cope (= *Bananogmius* Whitley, *Ananogmius* White & Moy-Thomas), is now regarded as a tselfatioid (Patterson 1967). Loomis (1900) and Stewart (1899) referred *Pachyrhizodus* to the Salmonidae. Boulenger (1910) also mentioned the Pachyrhizodontidae with the Salmonidae, although he expressed doubts concerning the systematic position of *Pachyrhizodus*. Woodward (1901) and Dunkle (1940) considered *Pachyrhizodus* as a 'spaniodontine elopid' and more recently it was placed with *Thrissopater* in a family separate from the Elopidae by Bertin & Arambourg (1958) and Applegate (1970). In considering the lower jaw structure of the American species of *Pachyrhizodus* Nelson (1973a) placed the genus as Teleostei *incertae sedis*.

The brief notes above concerning the history of the classification of these genera reveal two main points. Firstly, it is generally believed that *Notelops* is closely related to *Elops* whereas the other genera are removed from this lineage. Secondly, although *Rhacolepis*, *Thrissopater* and *Pachyrhizodus* may be separated from *Notelops* and *Elops* at the family level, the consensus of opinion favours placing the former genera near to the Elopidae with the implication that elopids are their nearest relatives.

My studies on the osteology of *Notelops*, *Rhacolepis*, *Thrissopater* and *Pachyrhizodus* suggest that these genera form an interrelated group of primitive teleosts that are very different from the elopids. These genera show several points of similarity with the protacanthopterygians, but there is insufficient evidence to justify their inclusion within that assemblage and they are left as Teleostei *incertae sedis*.

II. MATERIALS AND METHODS

Material used in the preparation of this work is in the collections of the British Museum (Natural History), London; Institute of Geological Sciences (Geological Survey Museum), London; Sedgwick Museum, Cambridge; University of Alberta (Geology Department); American Museum of Natural History, New York; and Southern Methodist University, Dallas, Texas. Specimens belonging to these institutions are identified by register numbers with the prefixes BM(NH), GSM, SM, UA, AMNH and SMU respectively.

Several specimens of *Notelops* and *Rhacolepis* were prepared by the transfer technique (Toombs & Rixon 1959). One specimen each of *Pachyrhizodus megalops* and *P. subulidens* were prepared in acetic acid as 'free-standing' specimens.

III. SYSTEMATIC DESCRIPTIONS

Suborder PACHYRHIZODONTOIDEI *nov.*

Definition. Primitive teleostean fishes, fusiform with terminal mouths and large jaws; frontals large, dermethmoid large, parietals small, parietal branch of supraorbital sensory canal absent, nasals short and tubular, supraoccipital small with weakly developed crest; supratemporal large; post-temporal fossa roofed;

orbitosphenoid and basisphenoid present, occipital condyle formed entirely by basioccipital, saccular region of neurocranium not inflated, parasphenoid without teeth or basipterygoid process, foramen for buccohypophyseal canal present; hyomandibular with single articulatory head, hyomandibular held vertically, endopterygoid with many small teeth, palatine without maxillary process; anterior and posterior ceratohyals separated by a narrow band of cartilage, numerous branchiostegal rays present; premaxilla with small dorsal process, one or two inner teeth and a single row of marginal teeth; maxilla long and shallow with a simple head fitting tightly against the premaxilla, a single splint-like supramaxilla, a single row of maxillary teeth; mandibular ramus shallow with a well-developed postarticular process, dentary and angular showing a 'reverse overlap'; large supraorbital meeting a large dermosphenotic, no separate antorbital, second and third infraorbitals fused together, posterior branch of infraorbital sensory canal within the dermosphenotic; two sclerotic ossicles; opercular apparatus complete; mesocoracoid present; pectoral fin held low on flank, pectoral splint absent; pelvic fins abdominal; vertebral centra pierced by notochordal canal, neural arches fused with centra except in anterior half of abdominal region, posterior parapophyses and haemal arches fused with centra, epineurals fused to neural arches, pleural ribs curved, supraneurals behind occiput; dorsal and anal fins acuminate, always distinct from caudal fin; caudal fin forked with 19 principal fin-rays; parhypural and lower hypurals fused to supporting centra, half-length neural spine on second preural centrum, first uroneural large, second uroneural reaching to first ural centrum, second ural centrum small, two epurals; scales cycloid with bone-cell spaces; lateral line complete.

Family **NOTELOPIDAE** *nov.*

Diagnosis. Pachyrhizodontoid fishes in which the skull roof is flat, ethmoid commissure bone enclosed, frontal margin not excavated, parietals medially united; subtemporal fossa present, intercalar large and extending anteriorly to form a prootic–intercalar bridge, trigeminal foramen opening into pars jugularis, myodome closed posteriorly, parasphenoid shallow beneath otic region; palatine long and dentigerous, ectopterygoid edentulous; lower jaw with separate angular, articular and retroarticular; dentary with several rows of teeth; gular plate present.

Genus ***NOTELOPS*** Woodward 1901

Diagnosis (emended). Notelopid fish in which the dermethmoid bears lateral projections, dilatator fossa with roof, pterotic without posterior spine, exoccipitals meeting above and below foramen magnum, large fenestra between autosphenotic and pterotic, lateral face of prootic without a crest above the orbitonasal foramen; anterior ceratohyal fenestrated; fourth and fifth infraorbitals fused together, posterior infraorbitals just reaching the preoperculum; preoperculum relatively small, operculum with oblique ventral margin, interoperculum short and deep; cleithrum expanded over fin insertion; origin of pelvic fin below posterior end of dorsal fin, pelvic splint-bone present; upper principal caudal fin-rays crossing hypural supports at a steep angle; scales small, marked by evenly spaced circuli around a central focus, a few scales extending over the base of the caudal fin.

Type species. *Rhacolepis brama* Agassiz.

Notelops brama (Agassiz)

(Figs 1–10)

1833 *Ambylpterus olfersi* Agassiz, **2** : 40.
1841 *Phacolepis brama* Agassiz : 83.
1841 *Calamopleurus cylindricus* Agassiz : 84.
1844 *Rhacolepis olfersii* (Agassiz) ; Agassiz, **4** : 293.
1844a *Rhacolepis olfersii* (Agassiz) ; Agassiz : 1012.
1887 *Rhacolepis brama* Agassiz ; Woodward : 539 ; pl. 46, fig. 1 ; pl. 47, fig. 4.
? 1895 *Calamopleurus cylindricus* Agassiz ; Woodward : 499.
1901 *Notelops brama* (Agassiz) Woodward : 27.
1907 *Calamopleurus cylindricus* Agassiz ; Jordan : 139 ; pl. 12.
1908 *Calamopleurus cylindricus* Agassiz ; Jordan & Branner : 16 ; pl. 3.
1908 *Notelops brama* (Agassiz) ; Jordan & Branner : 20 ; pl. 6, fig. 1.
1921 *Calamopleurus brama* (Agassiz) ; Jordan : 46 ; pl. 5, figs 1, 2 ; pl. 6, figs 1–3 ; pl. 7, figs 1–3.
1938 *Notelops brama* (Agassiz) ; D'Erasmo : 349.
1940 *Notelops brama* (Agassiz) ; Dunkle : 157.
1968 *Notelops brama* (Agassiz) ; Santos & Valença : 348, fig. 6.

Diagnosis (emended). *Notelops* reaching 600 mm total length; proportions (as percentage of standard length): head length 25, maximum depth of trunk 20–21, predorsal 46–49, prepelvic 55–58, preanal 78–80; fin-ray counts, D. iv, 11 or 12; A. ii, 6; P. 15–17; V. 12 or 13; approximately 60 preural vertebrae of which 19 or 20 are caudal; premaxilla equal to 22 per cent of length of upper jaw, with about 18 marginal teeth; maxilla with about 50 teeth; dentary with 3–4 rows of teeth, each row containing approximately 60 teeth; preopercular sensory canal with 3–5 ventral branches; diameter of orbit equal to 25 per cent of head length; 90–100 lateral line scales, 25–27 scales in transverse series anterior to dorsal fin, large axillary scale above pectoral fin.

Holotype. BM(NH) 15490, head plus cleithrum, Santana Formation (Aptian), Ceará, Brazil.

Material. Nineteen specimens in the British Museum (Natural History), four in the University of Alberta and one in the American Museum of Natural History were examined.

Formation and Locality. Not all specimens bear locality data but the distinctive matrix and preservation suggest that all come from the Santana Formation (Aptian), Ceará, Brazil.

Descriptive remarks. Dunkle (1940) presents a detailed account of the cranial osteology of *Notelops brama*, his description being based on serial sections of a single specimen. The following notes are based on several acid-prepared specimens and are intended to supplement or correct the description given by Dunkle. A description of the postcranial skeleton is also given.

Braincase. A comparison of Fig. 1 with that given by Dunkle (1904 : fig. 1A) shows a general similarity between the two reconstructions. I find the medially united parietals to be small and to have irregular margins. The path of the supraorbital sensory canal is shown in Fig. 1. The supraorbital sensory canal opens medially by two large pores. Posterolaterally the canal opens by several pores above the autosphenotic. There is no parietal branch or any evidence of pit-lines such as are seen in *Elops*.

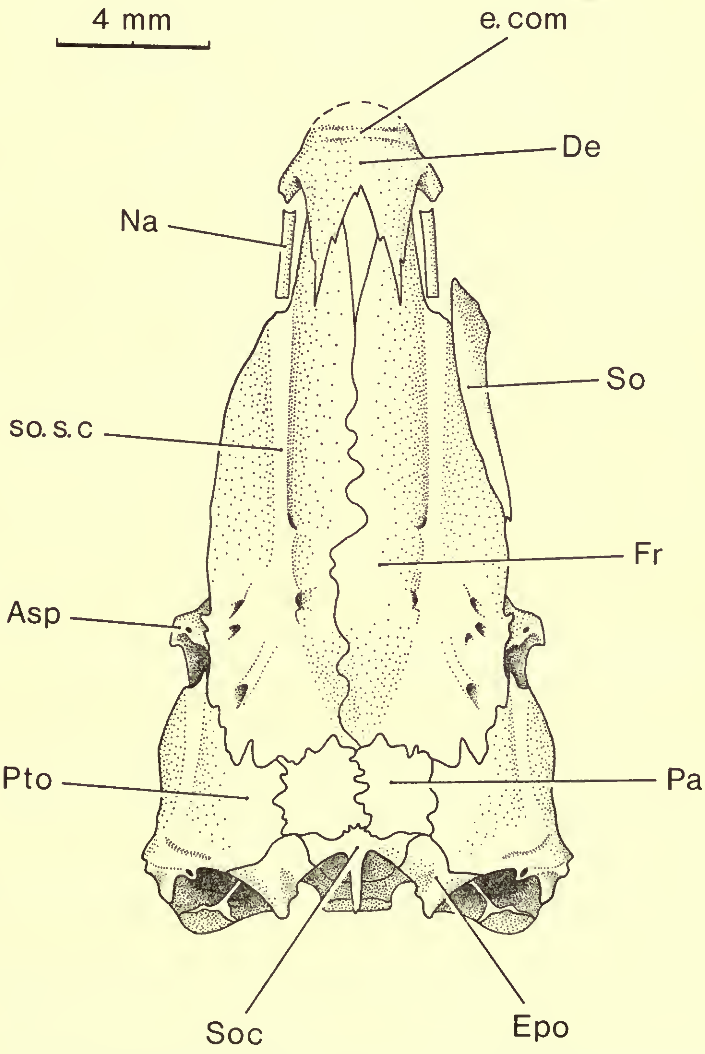

FIG. 1. *Notelops brama* (Agassiz). Restoration of braincase in dorsal view.

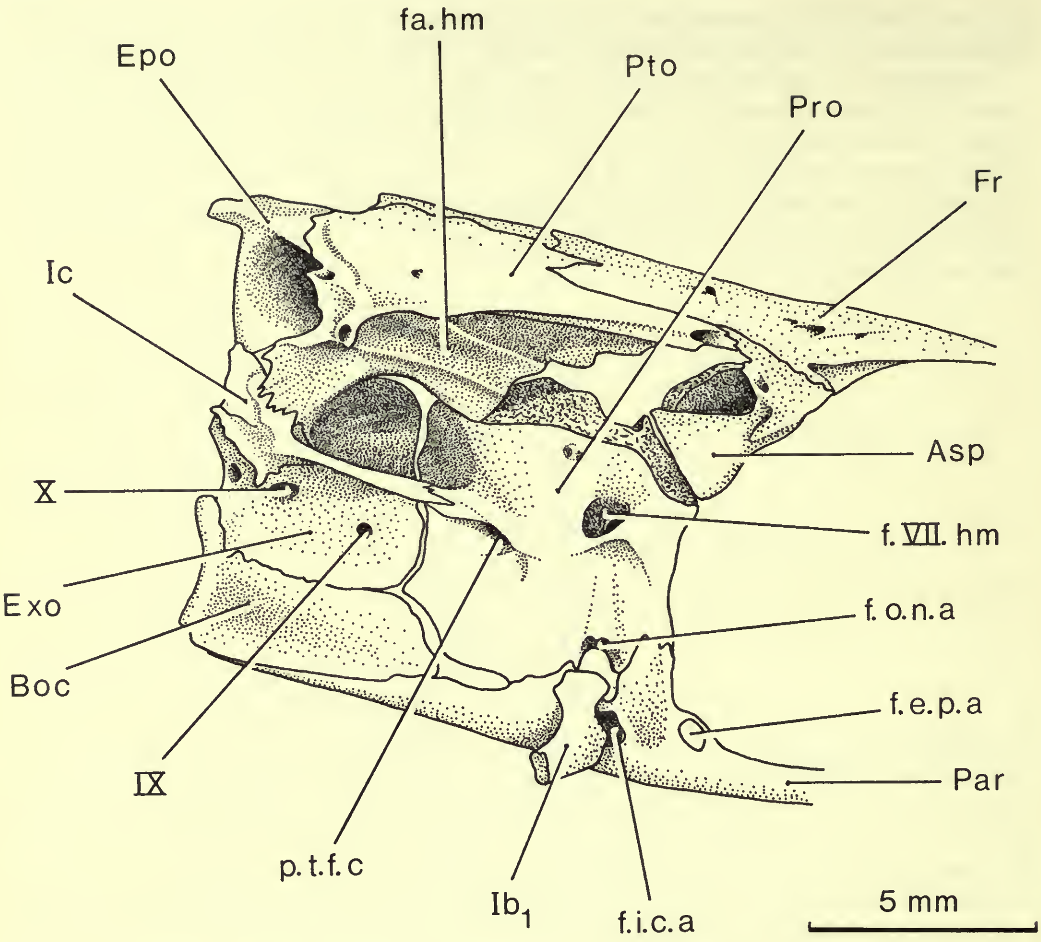

FIG. 2. *Notelops brama* (Agassiz). Postorbital part of braincase in right lateral view. Camera lucida drawing of UA 12021, a young individual.

Dunkle makes no mention of the foramen for the exit of the glossopharyngeal; it occurs in the usual position, on the lateral face of the exoccipital beneath the subtemporal fossa (Fig. 2, IX).

The intercalar (Fig. 2, Ic) is large, with an anteriorly directed strut which interdigitates with a ridge on the prootic, forming a prootic–intercalar bridge as in *Elops* and *Leptolepis dubia* (Blainville).

In the lateral face of the prootic Dunkle (1940 : 175, figs 1c, 5b) notes that the posterior palatine branch of VII left the prootic by a foramen which is separate from the foramen for the orbital artery. Bardack (1965 : 43) also notes a separate foramen in *Xiphactinus audax* Leidy. In BM(NH) P.1958 and UA 12021 there is no such separate foramen and presumably the posterior palatine branch of VII and the orbital artery shared a single foramen (Fig. 2, f.o.n.a). The presence of a single or double foramen is probably subject to individual variation.

The path of the abducens nerve, as reconstructed by Dunkle (1940 : fig. 6), is shown passing over the floor of the endocranial cavity to descend into the posterior myodome through the pituitary fossa. Such a path is unusual among 'lower teleosts'. All specimens examined here show a foramen within the prootic bridge, suggesting that the abducens followed a more usual course, directly through the floor of the endocranial cavity.

A feature worthy of note is the presence of a large fenestra between the autosphenotic and the pterotic (Fig. 2), in the wall of the dilatator fossa. This fenestra is present in all specimens examined. The margin of this fenestra in the largest specimen (UA 12020) is 'finished', suggesting an open area or one perhaps covered by membrane. If open, there was direct communication between the dilatator fossa and the post-temporal fossa. Similar fenestrae are seen in some specimens of *Tarpon atlanticus* (Cuvier & Valenciennes), *Brycon meeki* Eigenmann & Hildebrand (Weitzman 1962) and *Scleropages formosus* (Müller & Schlegel) (personal observation). The function of these fenestrae is not known.

On the orbital face there is a large, slit-like foramen straddling the suture between the autosphenotic and the pterosphenoid. The long axis of this foramen is inclined dorsomedially. The foramen leads from the orbit to the post-temporal fossa. A groove passes from the ventral lip of this foramen to the anterior opening of the jugular canal. The position of this foramen and the presence of the groove suggests that the ramus lateralis accessorius nerve ran up the orbital face and through the foramen. A smaller foramen, of unknown function, leading to the post-temporal fossa is seen within the pterosphenoid, close to the suture with the autosphenotic. The dorsal surface of the autosphenotic contains a small foramen (Figs 1, 2) which may have carried the otic branch of VII. It is not apparent where the otic nerve entered the autosphenotic, unless it ran into the bone with the ramus lateralis

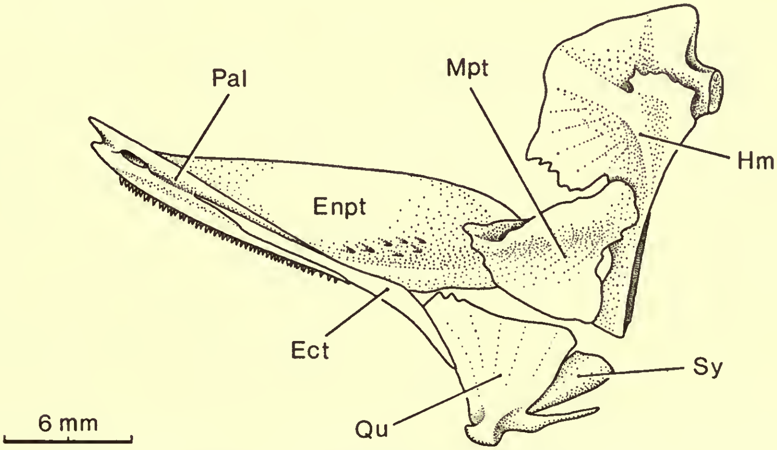

FIG. 3. *Notelops brama* (Agassiz). Left hyopalatine series in lateral view. Restoration based on UA 12021, a young individual.

accessorius. Dunkle (1940 : 175) suggests that the otic branch ran out of the braincase on the lateral face of the prootic together with the hyomandibular trunk of VII.

Hyopalatine series. The hyopalatine bones (Fig. 3) have been described by Dunkle (1940 : 182–184, fig. 8) but little mention was made of the dentition. The oral surface of the palatine bears many pointed teeth which are as large as those borne by the maxilla. There are 4–5 longitudinal rows of teeth. The ectopterygoid is edentulous, which is probably the result of the posterior extension of the palatine covering most of the oral surface of the ectopterygoid. The endopterygoid (entopterygoid of Dunkle 1940) bears many tiny, granular teeth which become slightly larger toward the endopterygoid/palatine interface.

Jaws. The upper jaw (Figs 4A, 6) is slender and long, reaching behind the orbit. The premaxilla (Fig. 4A, Pmx) is small and triangular and bears a ridge on the mesial surface. There are approximately 18 marginal teeth in a single row and there was probably a larger, inner premaxillary tooth anteriorly, since a socket (Fig. 4A) is seen in several specimens.

The maxilla is long and narrow, the head is simple and there is a very poorly developed palatine process. A single row of approximately 50 teeth is present.

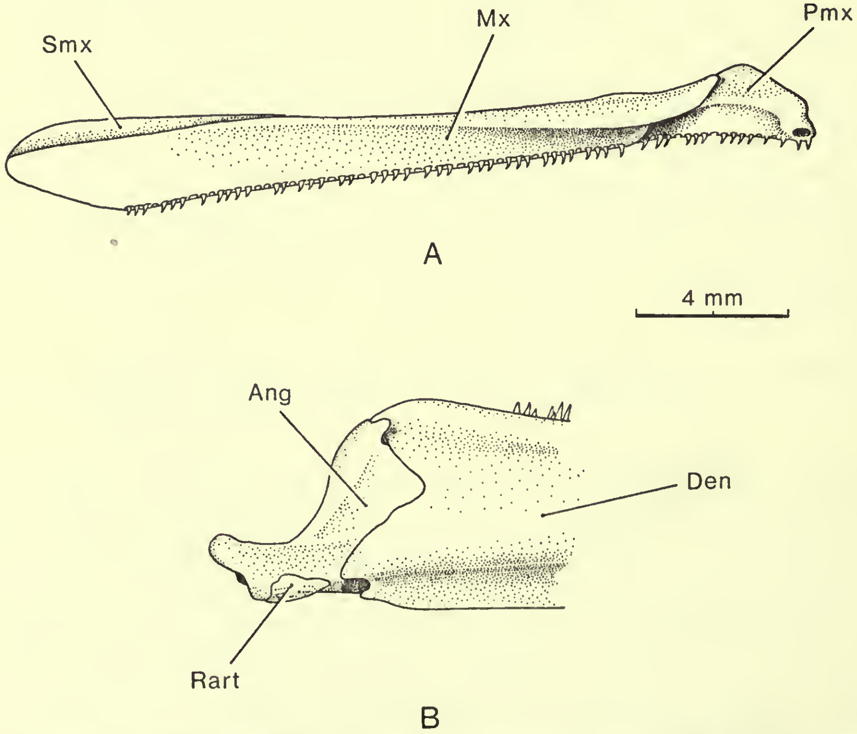

Fig. 4. *Notelops brama* (Agassiz). A: Restoration of left upper jaw in medial view. B: Posterior part of right mandibular ramus in lateral view. Camera lucida drawing of UA 12021, a young individual.

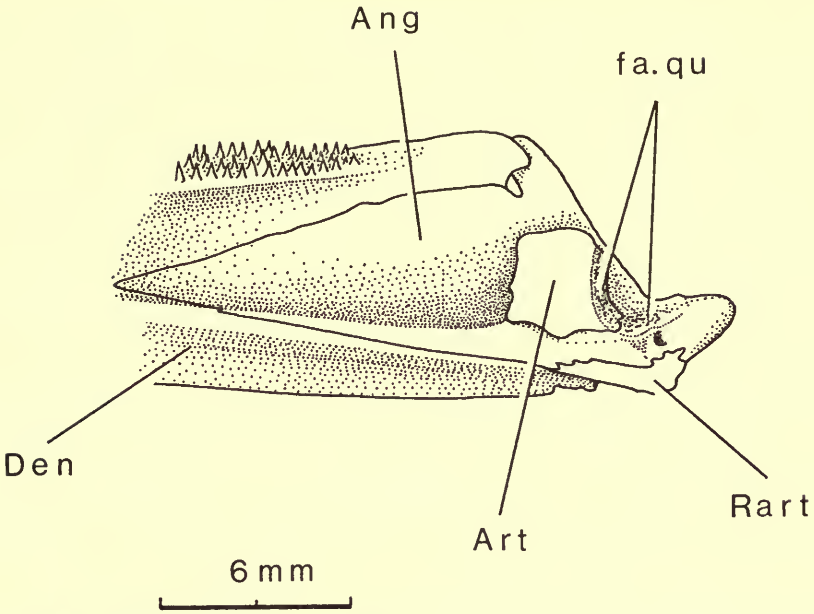

FIG. 5. *Notelops brama* (Agassiz). Posterior part of right mandibular ramus in medial view. Camera lucida drawing of UA 12022.

The bases of the teeth are fused with the maxilla and are covered laterally by a narrow ledge of thin bone. In some specimens the thin, overlapping ledge of the maxilla is broken. Hence these specimens appear to have larger teeth than those in which the ledge is complete. It may be of significance to note that Jordan & Branner (1908) distinguished *Notelops* from *Calamopleurus* (here placed in synonymy) on the supposedly larger teeth in the former.

The lower jaw (Figs 4B, 5, 6) is also long and shallow. The dentary occupies most of the mandibular length and bears a horizontal platform set with many pointed teeth. There are 3–4 longitudinal rows of teeth and, as in the maxilla, the bases of the outer teeth are covered by a narrow ledge of bone. The dentary teeth are slightly larger than those on the maxilla, being 1 mm long in a fish in which the mandible is 29 mm long. Posteriorly the angular has a small expression in lateral aspect. There is a well-developed postarticular process and a small, separate retroarticular. The angular is overlain over much of its length by the dentary, but in the region of the weakly defined coronoid process the angular portion overlaps the dentary. Nelson (1973b : 347) mentions that a similar 'reverse overlap' exists in some elopomorphs, in clupeomorphs and characoids.

The articular (Fig. 5, Art) is cuboid and rests on a ledge of the angular. The Meckelian cartilage probably lay in continuity with the anterior edge of the articular. The articular facet is divided into two parts. Most of the facet is developed on the posterior edge of the articular. The angular contributes a small horizontal portion of the facet and this lies directly behind the articular portion of the facet. The condition in *Notelops* is similar to that described for ichthyodectids by Nelson (1973a). Both *Notelops* and the ichthyodectids have a separate articular and angular, with the articulatory facet developed on both bones. According to Nelson (1973a : 11) this is an unusual condition in teleosts. However, the similarity in the composition of the articulatory facet cannot be taken as evidence of relationship between *Notelops* and ichthyodectids, because there is the possibility that an angular component of the facet may be primitive for many lower teleosts (Nelson 1973a).

The mandibular sensory canal runs through the length of the angular and dentary. Anteriorly the canal opens by one or two pores near the symphysis ; posteriorly it opens on the posterior face of the postarticular process. There is also a small foramen on the medial face of the angular (Fig. 5) immediately behind the articulatory facet.

Hyoid bar, branchiostegal rays and gill arches. As usual, the ceratohyal is ossified in two sections, the anterior being the longer and having a large fenestra ('Beryciform foramen' of McAllister 1968). In some specimens the posterior ceratohyal is also fenestrated. The dorsal and ventral hypohyals are each formed of spongy bone surrounded by a thin perichondral shell. The canal for the afferent hyoidean artery enters the ventral hypohyal and leaves the dorsal hypohyal on the mesial surface.

The exact number of branchiostegal rays is not known. There were certainly more than 18. Six or seven articulate with the posterior ceratohyal. The anterior branchiostegal rays are fine, those posteriorly being only slightly expanded in comparison with those anteriorly.

The gill arches could not be reconstructed accurately. Several acid preparations show ceratobranchial, epibranchial and infrapharyngobranchial elements. One specimen shows at least two hypobranchials, but none show basibranchials or a basihyal. No basibranchial tooth plates were seen. Dunkle (1940 : 158) notes that the dorsal segments of the branchial arches were present in this specimen but makes no mention of the ventral elements. Of the gill arch elements that are ossified and preserved there is a general similarity with the generalized pattern as seen in *Elops* (Forey 1973b, Nelson 1968a). The first infrapharyngobranchial (Fig. 2, Ib_1) is closely associated with the braincase where it is attached to the parasphenoid immediately behind the foramen for the internal carotid artery. The fourth epibranchial is expanded and has a deep notch for the fourth efferent branchial artery.

Small tooth-plates are associated with the ceratobranchials and at least the first three epibranchials. There are no well-developed gill rakers.

The urohyal is long and shallow and reaches from the mid-point of the mandible to beneath the middle of the interoperculum.

Circumorbital series. This consists of a supraorbital and four canal-bearing bones. There is no separate antorbital. The supraorbital (Figs 1, 6, So) is large, sutured to the dermosphenotic posteriorly and expanded anteriorly. The first infraorbital (lachrymal of authors) is somewhat expanded anteriorly (Fig. 6, Io_1). The presence of two infraorbitals and a dermosphenotic behind the eye represents a 'reduced' condition when compared to many 'lower teleosts' (see Nelson 1969, for the generalized teleost condition).

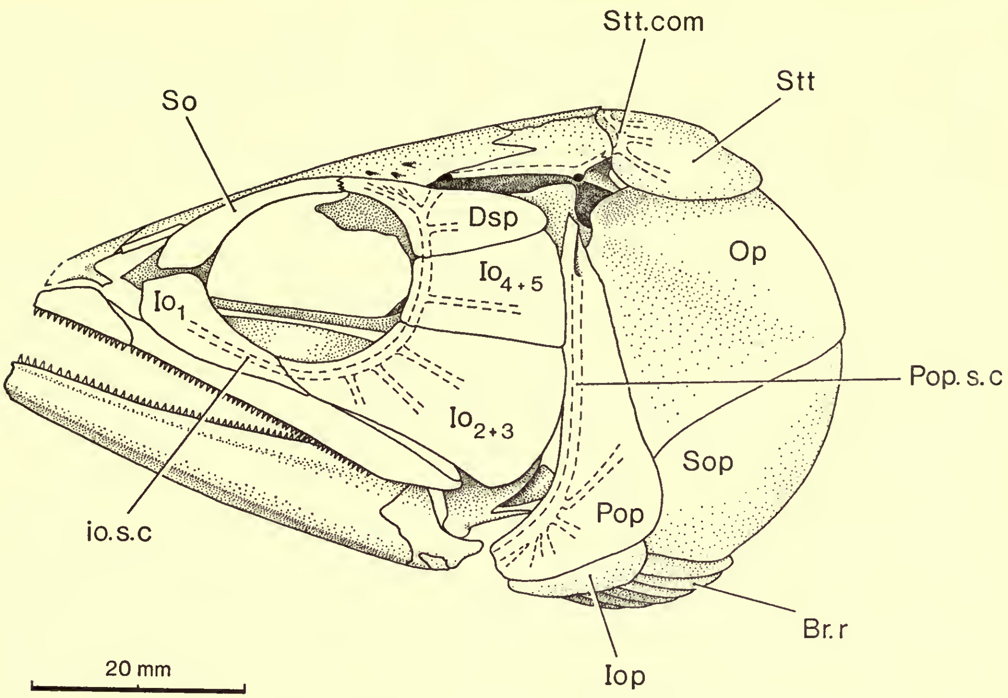

FIG. 6. *Notelops brama* (Agassiz). Restoration of cranium in left lateral view.

The large infraorbital bordering the posteroventral aspect of the orbit is interpreted as representing fused second and third infraorbitals (Fig. 6, Io_{2+3}) of a 'generalized teleost'. This interpretation is based on the size and extent of this element and the presence of three branches (hence at least three neuromasts) of the sensory canal. The two remaining posterior infraorbitals correspond to the fourth, fifth and sixth (the dermosphenotic) of a primitive teleost such as *Elops*. Thus, compared to the generalized teleost condition (Nelson 1969), the condition in *Notelops* represents one of fusion ; the possibility that an infraorbital has been lost is not considered as there is no well-documented case of the loss of an infraorbital in lower teleosts. Concerning the fusion pattern, two interpretations are worth consideration–either fusion between the dermosphenotic and the fifth infraorbital or fusion between the fourth and fifth infraorbitals (Fig. 6, Io_{4+5}). Support for the first interpretation is the presence of a posterior branch in the last infraorbital (here named the dermosphenotic). However, there does not appear to be another case of a dermosphenotic fusing with a fifth infraorbital in lower teleosts (see Nelson 1969 for diagrams). Support for the second interpretation is drawn from comparisons with *Rhacolepis* (a presumed close relative of *Notelops*) where there are distinct fourth and fifth infraorbitals. In *Rhacolepis* (see p. 157 and Fig. 20) the fourth infraorbital carries a branch of the main sensory canal while the fifth is without a branch. In *Notelops* the branch is seen in the lower half of the posterior infraorbital, and the depth of this infraorbital is comparable to the combined depth of the fourth and fifth infraorbitals in *Rhacolepis*. Although there is no firm evidence to choose one interpretation in preference to the other, the second is chosen here because it is compatible with possibilities of infraorbital fusion documented by Nelson (1969). The uppermost element is thus interpreted as representing only the dermosphenotic (Fig. 6, Dsp). The additional sensory canal branch is therefore regarded as a supernumerary branch (see p. 186); the pattern of branching is somewhat similar in the dermosphenotic of *Rhacolepis*.

Dunkle (1940 : fig. 9) shows a very small dermosphenotic separate from a larger infraorbital. I have regarded both as being the dermosphenotic. It is possible that the dermosphenotic ossifies from two centres in some individuals. This is known to happen in *Brycon meeki* (Weitzman 1962). However, it is also possible that the suture shown by Dunkle is, in fact, a breakage since the uppermost posterior infraorbital is strongly curved inward anterodorsally. The dermosphenotic, as reconstructed here, is comparable with the dermosphenotic of *Rhacolepis* and *Pachyrhizodus megalops*.

Opercular series. The opercular bones are shown in Fig. 6. In proportion they are different from those illustrated by Dunkle (1940 : fig. 9), who indicates the posterior margins by dashed lines implying a degree of uncertainty. The large curvature shown in the transverse vertical plane of the operculum is noteworthy. In some specimens the operculum is broken along a line running back from the level of the hyomandibular/operculum articulation. Woodward (1901 : 27) suggests that the operculum is subdivided, but I would agree with Jordan & Branner (1908 : 17) that this 'subdivision' is a line of frequent breakage.

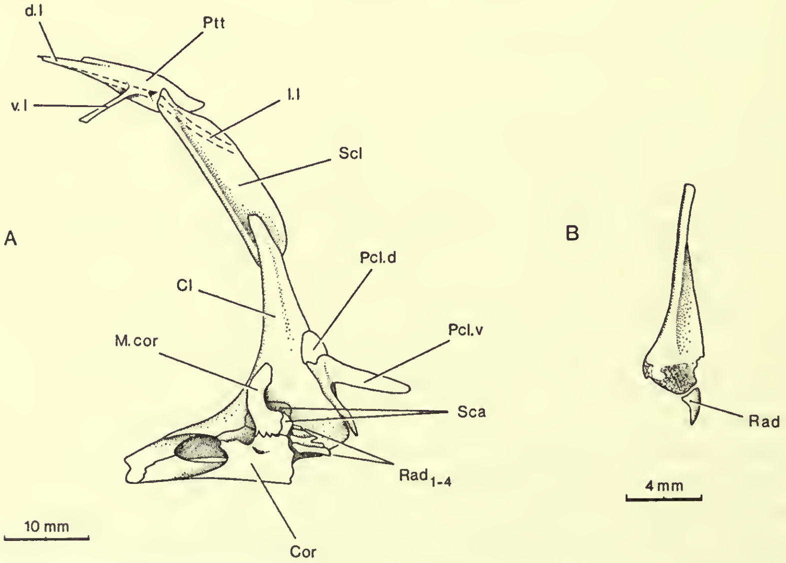

Fig. 7. *Notelops brama* (Agassiz). A: Restoration of right pectoral girdle in medial view. B: Pelvic bone and innermost radial of left side in dorsal view. Camera lucida drawing of UA 12021.

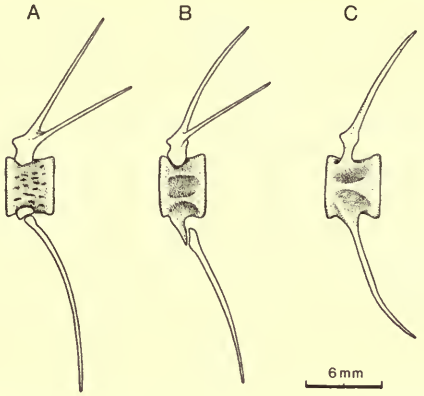

FIG. 8. *Notelops brama* (Agassiz). Vertebrae in left lateral view: A, from anterior abdominal region; B, from posterior abdominal region; C, from mid-caudal region.

Pectoral girdle and fin. The supratemporal (Fig. 6, Stt) is large and carries the supratemporal commissure. The post-temporal (Fig. 7A, Ptt) is produced to a stout dorsal or epiotic limb (Fig. 7A, d.l) and a narrow ventral or intercalar limb. The supracleithrum (Fig. 7A, Scl) is thickened along the anterior edge and this thickening is produced dorsally to a small process which fits into a depression on the underside of the post-temporal. The lateral line ran through the lateral margin of the post-temporal and obliquely through the upper portion of the supracleithrum.

The cleithrum (Fig. 7A, Cl) is the largest element of the girdle and is suturally united with the coracoid (Fig. 7A, Cor) anteriorly and posteriorly, leaving a large interosseus foramen (terminology of Starks 1930). The scapula (Fig. 7A, Sca) completely encloses the scapular foramen and the mesocoracoid (Fig. 7A, M.cor) is well developed forming the so-called 'mesocoracoid arch'. There are four proximal radials, two articulating with the scapula, two with the coracoid.

At least two postcleithra (Fig. 7A, Pcl) were seen. The dorsal postcleithrum is 'scale-like' and only slightly larger than the scales. The ventral postcleithrum is large and topographically divisible into two regions; a stout, ventrally directed rod and a thin, posteriorly directed lamina which resembles an axillary scale.

The pectoral fin (Fig. 9) is held almost horizontally and is composed of 15–17 rays. The outermost ray articulates directly with the scapula and is the only unbranched ray of the series. The longest fin-ray is the outermost and is equal to the length of sixteen abdominal vertebrae.

Pelvic girdle and fin. The pelvic fin originates beneath the posterior half of the dorsal fin. The pelvic bone (Fig. 7B) of either side is triangular and thickened along the lateral and posterior (transverse) margins. The transverse thickening was capped laterally and medially by cartilage. Three pelvic radials could be identified. The inner radial (Fig. 7B, Rad) is the largest and produced posteriorly as a narrow spur.

The pelvic fin (Fig. 9) is composed of 12–13 fin-rays, the outermost the longest (equal to the length of twelve abdominal vertebrae) and the only unbranched ray.

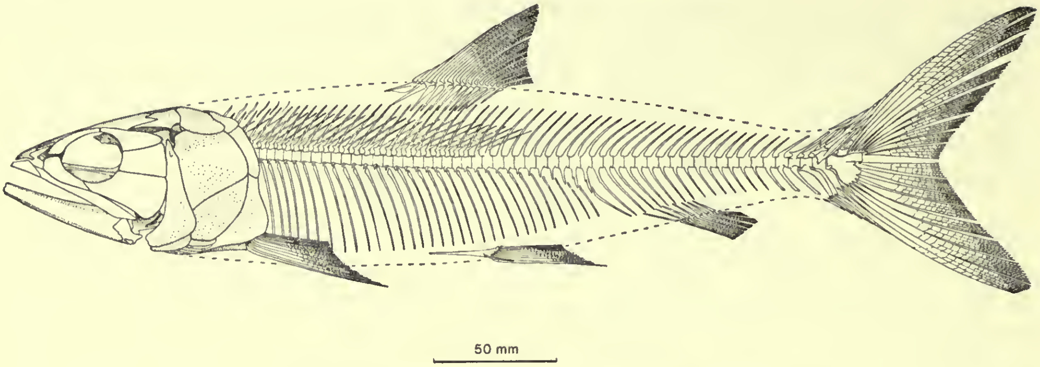

FIG. 9. *Notelops brama* (Agassiz). Entire fish, scales omitted.

Lateral to the upper half of the outermost ray there is a small, curved pelvic splint.

Vertebral column. The vertebral column is composed of approximately 60 vertebrae of which 19 or 20 are caudal. The anterior centra are deeper than long; those posteriorly are equally as long as deep. Each centrum is amphicoelous and pierced by a notochordal canal. Most of the centra are marked laterally by longitudinal ridges, but the first two or three are not ridged. The neural arches associated with the second to twenty-fifth vertebrae are autogenous. The last three neural arches and the haemal arches of Pu_{2-4} are also autogenous. The remaining neural arches, parapophyses and haemal arches are fused to the centra. The parapophyses of the last seven abdominal vertebrae increase in length with a corresponding decrease in rib length. The ribs (absent from the first centrum) are gently curved and slightly expanded proximally. The ribs do not reach the ventral midline. Short epineurals are fused with the first thirty neural arches. Several finer epineurals were seen behind this series in some specimens. No epicentral or epipleural intermusculars were seen.

The last three caudal vertebrae are modified to support the caudal fin and are described with the caudal skeleton. Approximately seven supraneurals are seen behind the occiput.

Dorsal and anal fins. The dorsal and anal fins may be seen in Fig. 9. The dorsal fin originates above the twenty-second vertebra and occupies a length of about ten vertebrae. The fin contains 15 or 16 rays supported by 12 or 13 pterygiophores; the fifth ray is the longest, being equal to the length of about thirteen vertebrae, and is the first branched ray of the series.

The anal fin is situated nearer to the caudal peduncle than to the pelvic fin. The fin originates below the forty-eighth vertebrae and is composed of eight rays. The base length of the anal fin is equal to the length of four vertebrae. The fin is slightly deeper than the base length. The third ray is the longest and the first branched ray of the series. There are seven pterygiophores.

Caudal skeleton and fin. The specimen (BM(NH) P.49084) on which this description is based is an acid-prepared specimen that is not associated with any cranial material. However, I am confident that it belongs to *Notelops brama* since the vertebral ornamentation is similar to complete specimens of this species and it is similar (as far as comparisons can be made) to the specimen identified as *Calamopleurus cylindricus* Agassiz (= *Notelops brama*) by Jordan (1907 : pl. 2) and again by Jordan & Branner (1908 : pl. 3).

The caudal fin-rays are supported by structures associated with three preural and two ural centra. The haemal spines on Pu_{1-3} are robust and the parhypural (Fig. 10, Ph) is characteristically angled ; a similarly angled parhypural is seen in *Ananogmius* and American species of *Pachyrhizodus*. The parhypural appears fused with Pu_1. The fused condition may represent either an ontogenetic phenomenon or co-ossification. The lower hypurals form a broad plate which is fused to the first ural centrum (Fig. 10, $U_1 + H_1 + H_2$). The hypural foramen (Fig. 10, fh) in the lower hypural plate marks the proximal division between H_1 and H_2, showing that the base of H_1 is the narrower (cf. elopiforms : Nybelin 1973, Forey 1973b). Only two upper hypurals (Fig. 10, H_3 and H_4) could be identified. H_3 and H_4 articulate with the second ural centrum. The gap in the specimen, left between H_4 and the uroneurals, suggests that more upper hypurals were present.

At least two uroneurals are present (Fig. 10, Un_{1-2}). The first is expanded proximally and covers much of the lateral face of Pu_1 ; the second is splint-like. A third uroneural may be present (Fig. 10). Articulating with Pu_1 there is a large arcual element (Fig. 10, $NaPu_1 + U_1$), which probably represents the first preural ural arch fused with the first ural neural arch. This interpretation is based on the width of

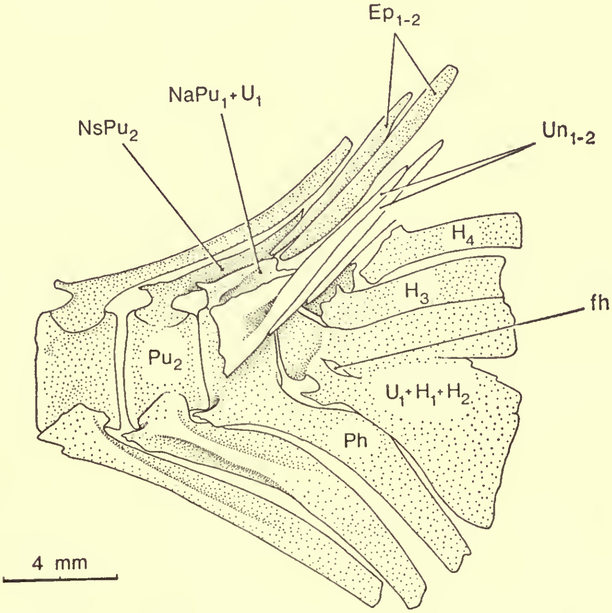

FIG. 10. *Notelops brama* (Agassiz). Caudal skeleton in left lateral view. Based on BM(NH) P.49084.

this arcual element. Pu_2 bears a neural arch and half-length neural spine (Fig. 10, $NsPu_2$). The neural spine associated with Pu_3 is full length. The neural arch elements are autogenous. There are two elongate epurals (Fig. 10, Ep_{1-2}).

The forked caudal fin contains 19 principal fin-rays. There are 9 branched principal rays in the upper lobe, 8 in the lower lobe. The inner principal fin-rays are profusely branched. The upper principal fin-rays overlie the hypural support at a steep angle. Preceding each of the outer principal fin-rays there are five procurrent rays.

Squamation. Cycloid scales are present over the body and extend onto the base of the tail. The scales are thin and circular, the focus is central and there are many evenly spaced circuli. The anterior field contains bone-cell spaces. The lateral line scales bear a small tube.

There are 90–100 scales in the lateral line series. Anterior to the caudal fin the transverse count appears to be 11 scales above the lateral line scale and 14–16 below. A large pectoral axillary scale is present.

Other species of Notelops. Jordan & Branner (1908) described a second species of *Calamopleurus* (= *Notelops*), *C. vestitus* from the Santana Formation of Ceará, Brazil. This species was said (Jordan & Branner 1908) to differ from the type species in showing larger scales and a smaller suboperculum. These authors suggested that these differences may warrant generic separation. Jordan (1921), in fact, separated *C. vestitus* from *Calamopleurus* and placed it in the genus *Brannerion* Jordan, demonstrating further points of difference from *Notelops brama.* He restudied the type specimen (No. 11, Rocha collection) of *Brannerion vestitum* (Jordan & Branner) and assigned a few other specimens to this species. According to him, *Brannerion vestitum* apparently differs from *Notelops brama* in many respects : the scales are much larger, the operculum has a convex ventral margin which is very oblique, the suboperculum is smaller, the mandible is projecting and the maxilla is short and reaches to beneath the middle of the orbit, the body is much shorter and deeper, the anal fin is long and originates beneath the dorsal fin and, if the specimen figured by Jordan (1921 : pl. 4, fig. 2) is correctly referred to *Brannerion vestitum,* the ribs and haemal spines are long and nearly straight. These differences are substantial. There are no details of the cranium or the caudal skeleton well enough known to confirm (or reject) the suggestion that *Brannerion vestitum* is related to *Notelops.* It may be significant that what is known of the body form, the shapes and sizes of the opercular bones, and the general appearance of the vertebral column (only a general impression is figured by Jordan) is similar to those areas in *Hiodon.* Clearly, very much more detailed anatomy needs to be known to substantiate such a claim.

Family **PACHYRHIZODONTIDAE** Cope 1872

DIAGNOSIS (emended). Pachyrhizodontoid fishes in which the skull roof is broad and convex in the otic region, bone-enclosed ethmoid commissure absent, frontal margin excavated above autosphenotic spine, parietals separated by supraoccipital ; subtemporal fossa absent, intercalar small, not reaching prootic, trigeminal foramen opening directly to orbit, myodome open posteriorly, parasphenoid deep beneath otic region ; palatine short, ectopterygoid with teeth ; lower jaw with anguloarticular and retroarticular ; dentary with single row of teeth ; gular plate absent.

Genus ***RHACOLEPIS*** Agassiz 1841

1841 *Phacolepis* Agassiz : 83.

DIAGNOSIS (emended). Pachyrhizodontid fishes in which the skull roof is without a marked depression at the level of the autosphenotics, dermethmoid with lateral projections, dilatator fossa without a complete roof, pterotic produced to a short spine ; exoccipitals meeting above but not below foramen magnum, endochondral elements of the otic region of the braincase united by interdigitating sutures, no fenestra between autosphenotic and pterotic, lateral face of prootic with a well-developed ridge running from the posterior opening of the jugular canal to the orbital artery foramen, vomer with two recurved teeth ; ectopterygoid with short dorsal process and a single row of pointed teeth ; anterior ceratohyal fenestrated ; posterior infraorbitals overlying preoperculum ; preoperculum with truncated vertical limb and produced to a spine-like process anteroventrally, operculum with oblique ventral margin, interoperculum longer than deep ; posterior margin of cleithrum excavated opposite fin insertion ; caudal fin-rays not crossing hypurals at a steep angle ; scales small, ovoid and marked by circuli in the dorsal and ventral fields, posterior field with fine radiating ridges, focus central, scales extending over the base of the caudal, dorsal and anal fins.

TYPE SPECIES. *Rhacolepis buccalis* Agassiz.

Rhacolepis buccalis Agassiz

(Figs 11–24)

1841 *Rhacolepis buccalis* Agassiz : 83.
1844a *Rhacolepis buccalis* Agassiz : 1011.
1887 *Rhacolepis buccalis* Agassiz ; Woodward : 539 ; pl. 46, figs 2–7 ; pl. 47, figs 1–3.
1901 *Rhacolepis buccalis* Agassiz ; Woodward : 30.
1908 *Rhacolepis buccalis* Agassiz ; Jordan & Branner : 21 ; figs 12, 13 ; pl. 6, fig. 2.
1921 *Rhacolepis buccalis* Agassiz ; Jordan : 62 ; pl. 8, figs 1–5.
1968 *Rhacolepis buccalis* Agassiz ; Santos & Valença : 348, fig. 6.

DIAGNOSIS (emended). *Rhacolepis* reaching 250 mm total length ; head length equal to 22 per cent of standard length, maximum depth trunk equal to 17–19 per cent of standard length ; fin-ray counts, P. 16 or 17, V. 10 or 11 ; estimated total number of preural vertebrae 55–65 of which about 20 are caudal ; paired fins short, pelvic fin originating behind the level of the dorsal fin and situated nearer to the caudal peduncle than to the pectoral fin ; posterior infraorbitals twice as broad as deep ; diameter of orbit equal to about 20 per cent of head length ; premaxilla equal to 21 per cent of length of upper jaw, with about 10 marginal teeth ; maxilla with about 35 teeth ; dentary with about 35 teeth ; preopercular sensory canal with 8–10 ventral branches ; about 90 lateral line scales, approximately 20 scales in transverse series anterior to dorsal fin, scales deeper than long, deeply overlapping.

HOLOTYPE. BM(NH) P.4314a, a crushed head, Santana Formation (Aptian), Ceará, Brazil.

MATERIAL. Twenty-six specimens in the British Museum (Natural History), four in the University of Alberta and one in the American Museum of Natural History were examined.

FORMATION AND LOCALITY. Santana Formation (Aptian), Ceará, Brazil.

DESCRIPTION. The species here referred to the genus *Rhacolepis* Agassiz have never been satisfactorily described. Woodward (1887) gives a composite description with *Notelops brama*, implying that the two genera are closely similar. In fact, the genera are rather different, with *Rhacolepis* being more advanced in several respects (p. 192). The following description is an account of the osteology of *Rhacolepis buccalis* (as representative of the genus), and will serve to emphasize the points of difference from the osteology of *Notelops*.

Braincase. The braincase is long and shallow, being three times as long as deep. The greatest width of the braincase occurs at the level of the autosphenotic (cf. *Notelops*) and is equal to two-thirds of the braincase length. The roofing bones of the skull are smooth, except for the ridges associated with sensory canals and

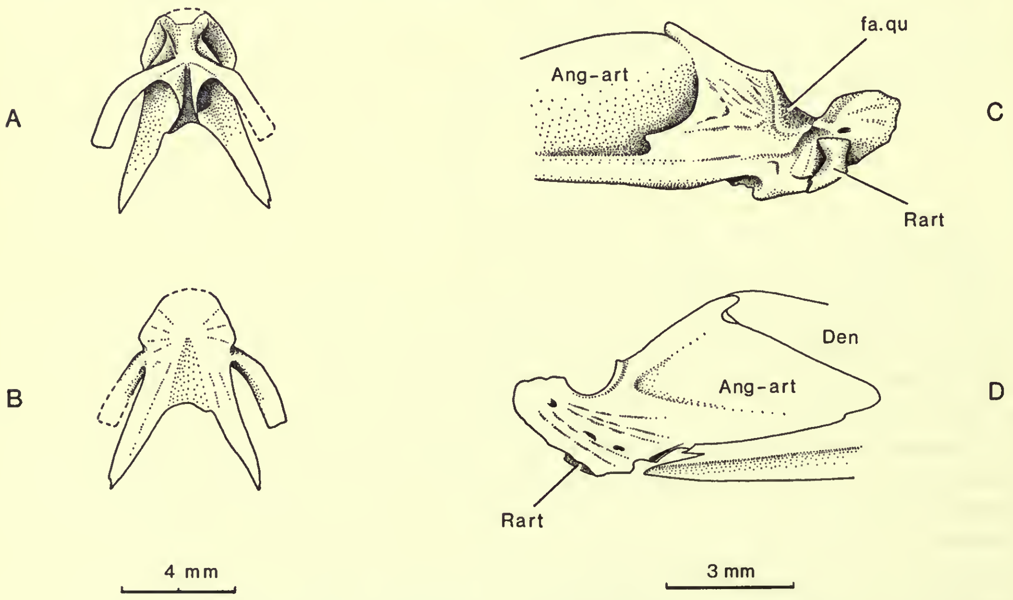

FIG. 11. *Rhacolepis buccalis* Agassiz. A: Dermethmoid in ventral view. B: Dermethmoid in dorsal view. Camera lucida drawings of isolated bone from UA 12026. C: Posterior portion of angulo-articular in medial view. Camera lucida drawing from UA 12026; retroarticular from AMNH 4617. D: Posterior portion of right mandibular ramus. Based on UA 12026 and AMNH 4617.

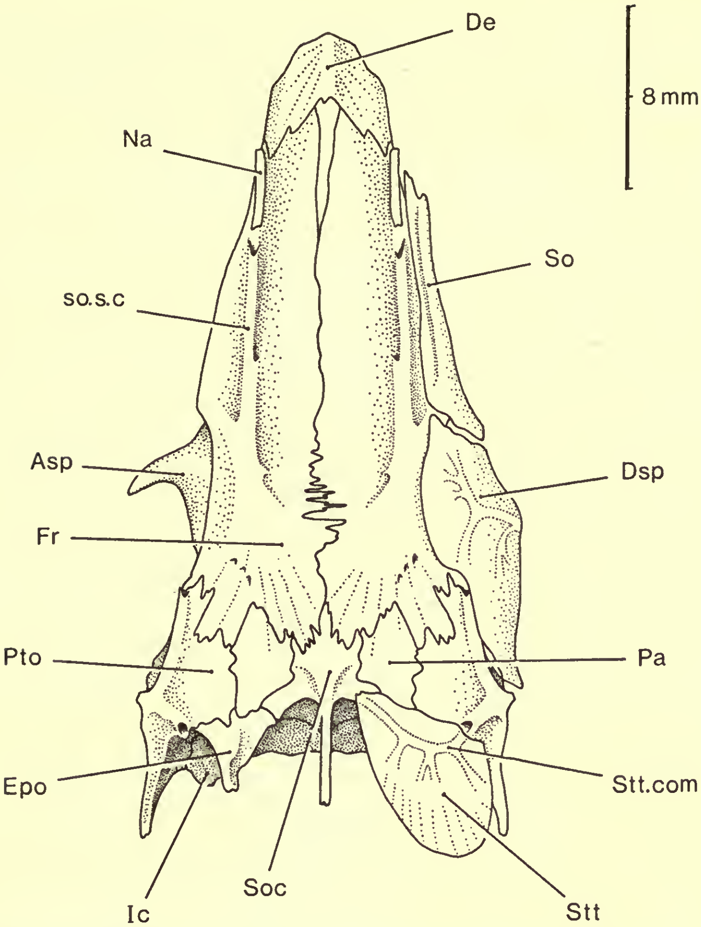

FIG. 12. *Rhacolepis buccalis* Agassiz. Restoration of skull roof. Supraorbital, dermosphenotic and supratemporal shown on right side only.

smaller radiating ridges on the dermethmoid and the posterior limits of the frontals. In unprepared specimens the dermal bones are much smoother than the corresponding elements in *Notelops*.

The dermethmoid is of complex shape. The main body of the dermethmoid (Fig. 11A, B; Fig. 12, De) forms a broad, triangular plate which overlies the anterior ends of the frontals. Ventrally (Fig. 11A), the dermethmoid bears paired ventrolateral projections which are longer than those in *Notelops*. Anterior and posterior to each lateral projection, the ventral surface is raised into 'cones', the tips of which converge at the base of the ventrolateral projections. The shape of the dermethmoid appears to change during ontogeny, the smaller (presumably younger) individuals having a narrower dermethmoid with relatively larger ventrolateral projections. The entire structure here termed the dermethmoid appears to be composed of dermal bone; if there is a perichondral component, it is certainly not recognizable. There is no evidence that the ventrolateral projections are ontogenetically separate from the main body (cf. Weitzman 1967 on *Megalops*). The dermethmoid bears no evidence of an ethmoid commissure (cf. *Notelops*; Fig. 1, e.com).

The frontal (Fig. 12, Fr) meets its antimere over most of its length, except anteriorly where the cartilage of the ethmoid region was presumably present. The interfrontal suture becomes complex in the epiphyseal region, a point of distinction from that of *Notelops* (Fig. 1). Above the orbit the frontal is raised in the midline so that together the frontals form a median ridge (see also Woodward 1887: pl. 46, fig. 3). Such a ridge is not seen in *Notelops*. The supraorbital sensory canal (Fig. 12, so.s.c) opens medially above the epiphyseal region and at the mid-orbital level. Anteriorly the canal opens onto the surface of the frontal. The sensory canal continued forward in a small, tubular nasal (Fig. 12, Na). The posterior branches of the supraorbital sensory canal could not be accurately determined. Three small pores are generally seen (Fig. 12) but there is no major branch suggesting a linkage between supraorbital and infraorbital sensory canals. On the basis of several suitably prepared specimens, I conclude that there was no supraorbital–infraorbital canal connection. The lateral margin of the frontal is excavated above the autosphenotic spine, as in the English species of *Pachyrhizodus*. This results in a partially unroofed dilatator fossa. In *Notelops* the frontal margin is not excavated and the dilatator fossa is roofed. Posteriorly the margin of the frontal is more irregular than in *Notelops*.

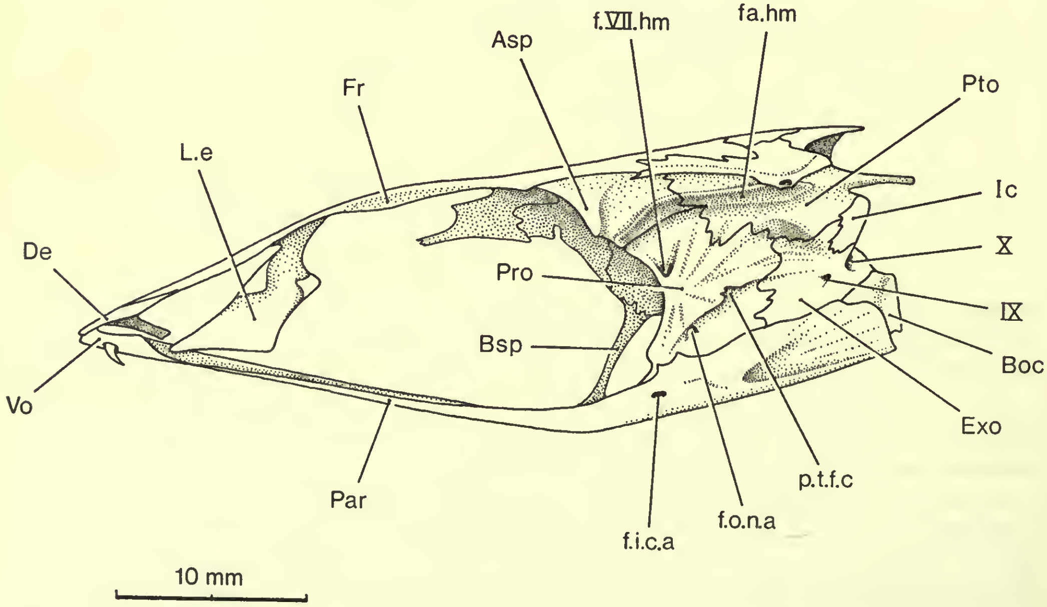

FIG. 13. *Rhacolepis buccalis* Agassiz. Braincase in left lateral view. Based on BM(NH) P.49084.

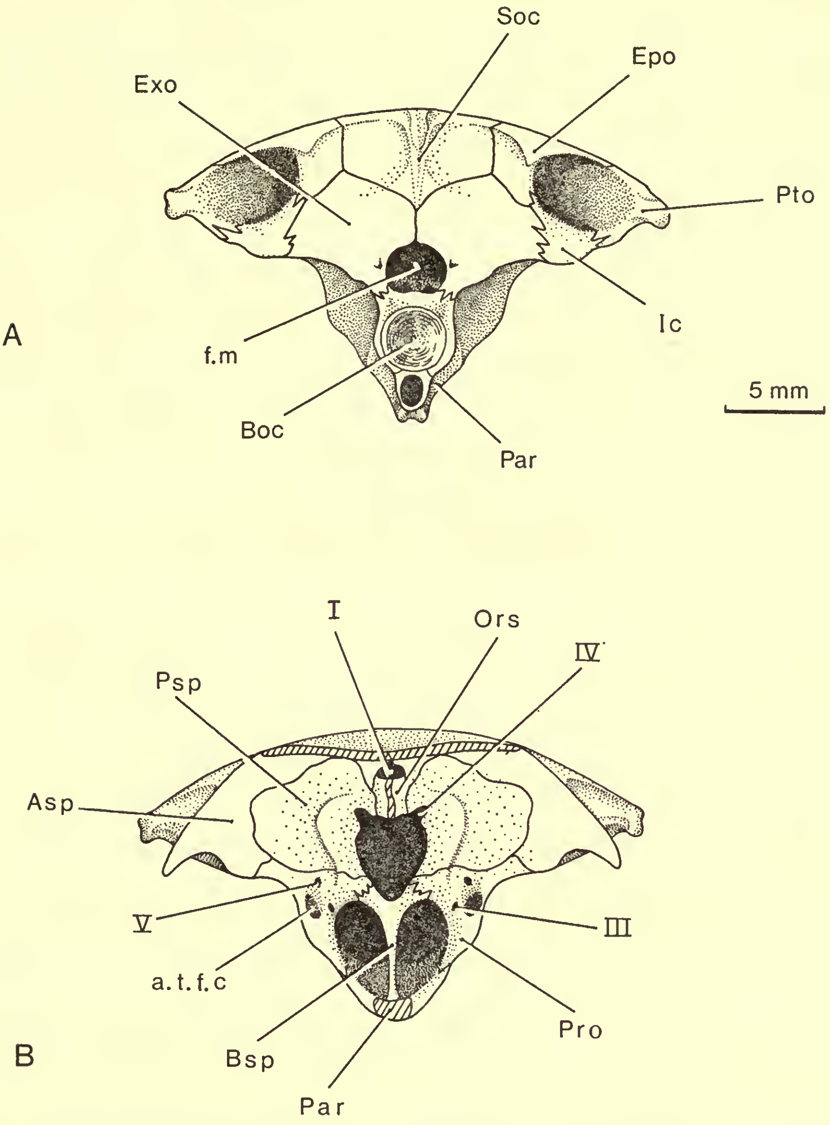

Fig. 14. *Rhacolepis buccalis* Agassiz. A : Braincase in posterior view. B : Orbital view of the postorbital part of the braincase. Both based on BM(NH) P.49084.

The pterotic (Figs 12, 13, 14A, Pto) constitutes a smaller proportion of the skull-roof area than in *Notelops*. Posteriorly the pterotic is produced as a prominent spine, absent in *Notelops*. The temporal sensory canal runs at the lateral margin of the pterotic and opens laterally to receive the preopercular sensory canal. From here the temporal canal runs posteromedially to open above the post-temporal fossa. In *Notelops* (Fig. 1) it may be seen that the temporal canal runs away from the lateral margin of the pterotic, leaving a small 'ledge' of bone overlying the dilatator fossa. Topographically, this is missing in *Rhacolepis* and the posterior area of the dilatator fossa is unroofed. The lateral wall of the pterotic composes the posterior halves of the dilatator fossa and the hyomandibular facet (Figs 13, 15, fa.hm). The parietals (Fig. 12, Pa) are small, irregular, and are separated by the supraoccipital. The separated parietals of *Rhacolepis* are contrasted with the medially united condition in *Notelops*.

The supraoccipital (Figs 12, 14A, Soc) bears a well-developed spine which continues forward as a ridge upon the main body of the bone. The epiotic (Figs 12, 14A, Epo) is produced as a well-developed process which bears a ridge receiving the epiotic (dorsal) limb of the post-temporal.

The exoccipital (Figs 13, 14A, Exo) is pierced by foramina for the vagus and glossopharyngeal nerves, as in *Notelops*. In *Rhacolepis* these foramina are closer together than in *Notelops*. The intercalar (Figs 13, 14A, Ic) is less complex than in *Notelops*, and there is no prootic–intercalar bridge. In *Rhacolepis* the intercalar is smooth and interdigitates with the exoccipital, pterotic and epiotic. In posterior view (Fig. 14A) the intercalar may be seen to form the ventral margin of the opening to the post-temporal fossa.

The basioccipital (Figs 13, 14A, Boc) forms the occipital condyle and the ventral margin of the foramen magnum. In *Notelops* the exoccipitals meet below the foramen magnum (Dunkle 1940 : fig. 1B). Immediately behind the foramen magnum the dorsal surface of the basioccipital is marked by a pair of pits (UA 12026), presumably for the reception of neural arches – these latter elements were not seen. The presence of the pits suggests that a centrum element has been incorporated into the basioccipital of *Rhacolepis*. A similar situation exists in *Pachyrhizodus megalops*. Pits are not present on the basioccipital of *Notelops*, although it is still possible that the basioccipital contains a centrum element. In lateral view (Fig. 13) the basioccipital does not appear to be as large as in *Notelops* (Fig. 2), but this is because the parasphenoid of *Rhacolepis* has a broad overlap with the basioccipital.

The prootic (Figs 13, 14B, 15, Pro) is, as usual, a large element. Laterally, the prootic meets the pterotic, exoccipital and basioccipital in an interdigitating suture ; a point of distinction from the corresponding sutures of *Notelops* (Fig. 2 and Dunkle 1940 : fig. 1C). As in *Notelops*, the lateral face of the prootic is pierced by three foramina, each leading into the jugular canal. Dorsally, there is a large foramen for the exit of the hyomandibular trunk of the facial (Figs 13, 15, f.VII.hm) ; ventrally there is a foramen for the entry of the orbital artery (Fig. 13, f.o.n.a) ; posteriorly there is a foramen for the exit of the jugular (head) vein (Fig. 13, p.t.f.c). The posterior palatine branch of the facial descended through the prootic bridge into the myodome, and then pierced the lateral wall of the myodome (formed by the prootic) at the level of the foramen for the orbital artery. Therefore, in lateral view, the foramen for the orbital artery also opens to the myodome. In *Rhacolepis* there is a ridge on the lateral face of the prootic, running from above the foramen for the head vein anteroventrally to above the foramen for the orbital artery. Presumably this ridge served as a site of attachment for part of the superficial branchial musculature : such a ridge is not present in *Notelops*. There is no

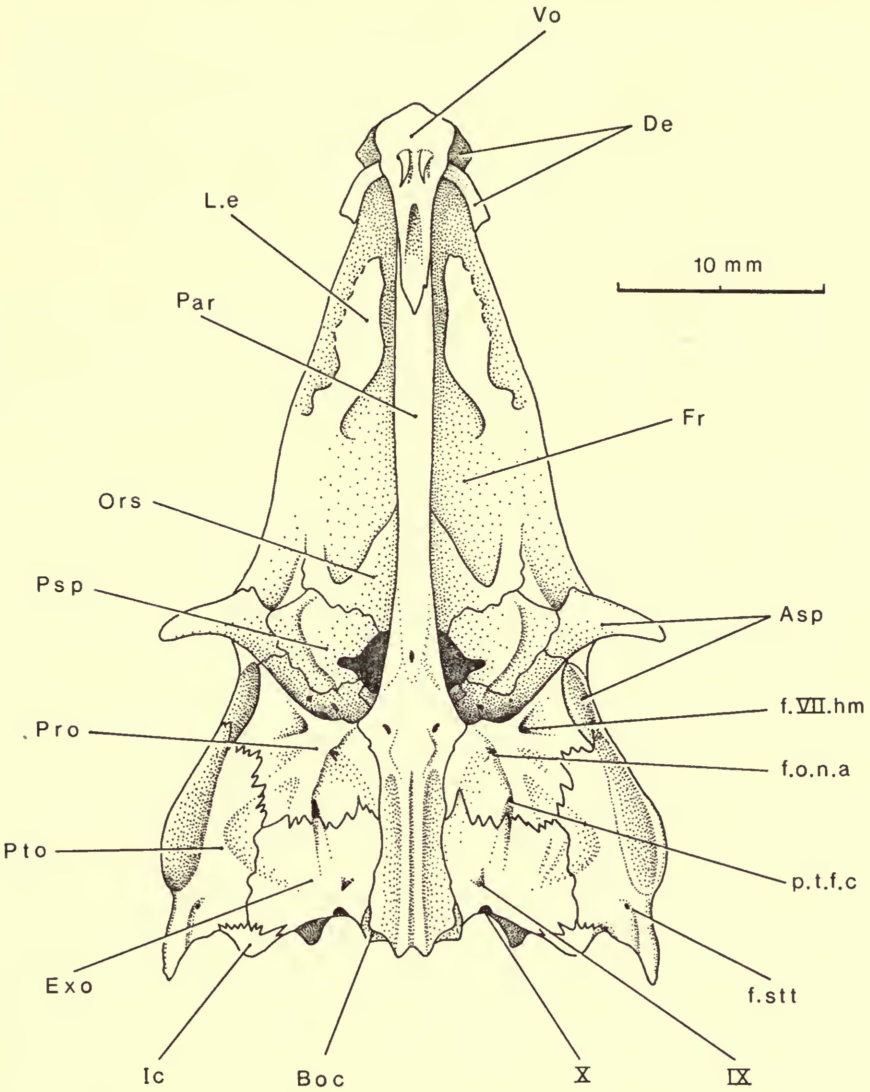

FIG. 15. *Rhacolepis buccalis* Agassiz. Braincase in ventral view. Based on BM(NH) P.49084.

well-defined subtemporal fossa in *Rhacolepis* (cf. *Notelops*), only a broad, shallow depression remains (see p. 194 for a possible functional explanation).

The anterior, orbital face of the prootic (Fig. 14B, Pro) is pierced by three foramina. Laterally, there is a foramen (Fig. 14B, a.t.f.c) for the jugular vein, orbital artery and the buccal and superficial ophthalmic branches of the facial. Dorsal to this large foramen is a smaller foramen (Fig. 14B, V) for the trigeminal nerve. In *Notelops* both the anteriorly running branches of the facial and the trigeminal run into the jugular canal before passing into the orbit. It appears that in *Rhacolepis* the prefacial commissure, separating the facial from the trigeminal foramina, is so wide as to ' displace ' the trigeminal foramen anteriorly, beyond the limits of the lateral commissure. It is of interest to note that *Pachyrhizodus megalops* is similar to *Rhacolepis* in this respect (p. 167). A third foramen, the occulomotor foramen (Fig. 14B, III), lies medial to the anterior opening of the jugular canal. The profundus nerve ran through the trigeminal foramen, or in a few individuals examined through a separate foramen situated very near the trigeminal foramen. The abducens ran through the prootic bridge, as in *Notelops*.

The autosphenotic (Figs 12, 13, 14B, 15, Asp) is produced as a prominent spine and also forms the anterior half of the facet for the hyomandibular. There is no fenestra between the autosphenotic and pterotic as there is in *Notelops* (Fig. 2). Similarly there is no large foramen in the orbital face of the autosphenotic as there is in *Notelops* (p. 133). A foramen for the otic branch of the facial could not be identified.

The pterosphenoid (Figs 14B, 15, Psp) is large and is marked by a prominent crest which runs up and forward. The superficial ophthalmic branches of the facial and trigeminal ran along the lateral edge of this crest. The pterosphenoid forms much of the lateral margin of the optic foramen and, as may be seen in Fig. 14B, a deep notch in the margin shows where the trochlear (IV) left the endocranial cavity.

The orbitosphenoid (Ors) and basisphenoid (Bsp) are unremarkable ; the shapes, relative sizes and position may be seen in Figs 13, 14B and 15.

The lateral ethmoid (Figs 13, 15, L.e) is thin and appears to be formed entirely by perichondral bone, a point of distinction from the lateral ethmoid (parethmoid of Dunkle 1940 : 172) of *Notelops*, in which there is a thin layer of endochondral bone lining perichondral bone. The lateral ethmoid of *Rhacolepis* spreads anteroventrally as a broad sheet, ending beneath the ventrolateral projections of the dermethmoid.

The vomer (Fig. 15, Vo) is expanded anteriorly, where it meets the dermethmoid. Posteriorly, the vomer passes into a grooved lamina which underlies the anterior end of the parasphenoid. The vomer bears two pointed teeth (Fig. 15) set into sockets in the head of the bone. The teeth are larger than those borne by the dermal jaw bones and are recurved. Between the vomer, dermethmoid and lateral ethmoids there is a space, suggesting that the internasal septum and nasal capsules were cartilaginous.

The parasphenoid (Figs 13, 14, 15, Par) is long, narrow beneath the orbit and deep beneath the otic region. There is a marked angle in the parasphenoid at the basisphenoid insertion. At this point the parasphenoid is pierced by an oblique median canal, the buccohypophyseal canal. The foramen for the internal carotid artery (Fig. 13, f.i.c.a) occurs beneath the poorly-developed ascending wing. Immediately posterior to this foramen is a low prominence which is the point of articulation for the first infrapharyngobranchial. The posterior part of the parasphenoid is marked by a mid-ventral groove and broader lateral grooves. Posteriorly, the ventral surface of the parasphenoid does not meet the basioccipital resulting in the myodome being open posteriorly. This opening may be seen in Fig. 14A ; such a foramen is not present in *Notelops*.

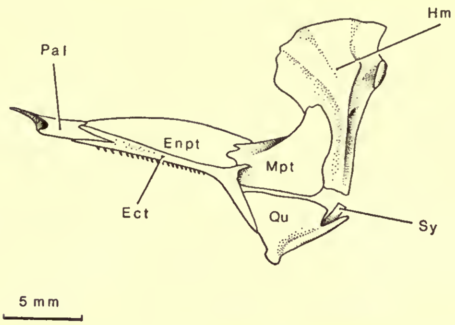

FIG. 16. *Rhacolepis buccalis* Agassiz. Restoration of the left hyopalatine series in lateral view.

Hyopalatine series. The hyomandibular (Fig. 16, Hm) has a broad head and a moderately wide shaft that is held vertically. A ridge runs on the outer face of the shaft but is not as well developed as it is in *Notelops*.

The metapterygoid (Fig. 16, Mpt) bears a well-defined ridge which divides the bone into an inner horizontal and an outer vertical portion. The latter overlaps a thin lamina of the hyomandibular. The quadrate (Fig. 16, Qu) has the shape of an equilateral triangle and is thus different from that of *Notelops* (Fig. 3). The dorsal margin is only weakly emarginated for the reception of the symplectic (Fig. 16, Sy). The endopterygoid (Fig. 16, Enpt) is similar to that in *Notelops* and bears a similar dentition of many fine granular teeth (Fig. 18).

The ectopterygoid (Fig. 16, Ect) is narrow and produced as a dorsal process just above the metaptergoid. Unlike that of *Notelops*, the ectopterygoid bears a single row of approximately 20 small, recurved teeth, and thus forms a functional part of the oral surface of the palate. The palatine (Fig. 16, Pal) is small (cf. *Notelops*, Fig. 3) and is represented by a dorsoventrally flattened tube of bone. Anteriorly the ' tube ' is open anterolaterally; posteriorly the opening is filled by the ectopterygoid and the endopterygoid. There are no teeth on the palatine. The terminology of the element here called the palatine is in doubt. The element clearly represents at least the autopalatine of a teleostean fish such as *Tarpon*. There is no separate dermopalatine, but neither is there evidence of fusion between an autopalatine and an edentulous dermopalatine or evidence of loss of the dermopalatine. The palatine of *Notelops* represents the result of fusion between autopalatine and dermopalatine elements.

Dermal upper jaw. The upper jaw reaches back to the hind margin of the orbit and is composed of the premaxilla, maxilla and a single supramaxilla. The premaxilla (Fig. 17A, B) is equal to one-fifth of the total jaw length, and is almost as deep as long. The premaxilla consists of a stout lower portion with a thin semicircular wing which projects dorsally and abuts onto the dermethmoid. Anteriorly and dorsally the premaxilla shows an external convexity. In medial view (Fig. 17A) a V-shaped groove is seen posteriorly and a deep pocket, which is open dorsally, may be seen anteriorly. A premaxilla–ethmoid ligament may well have been

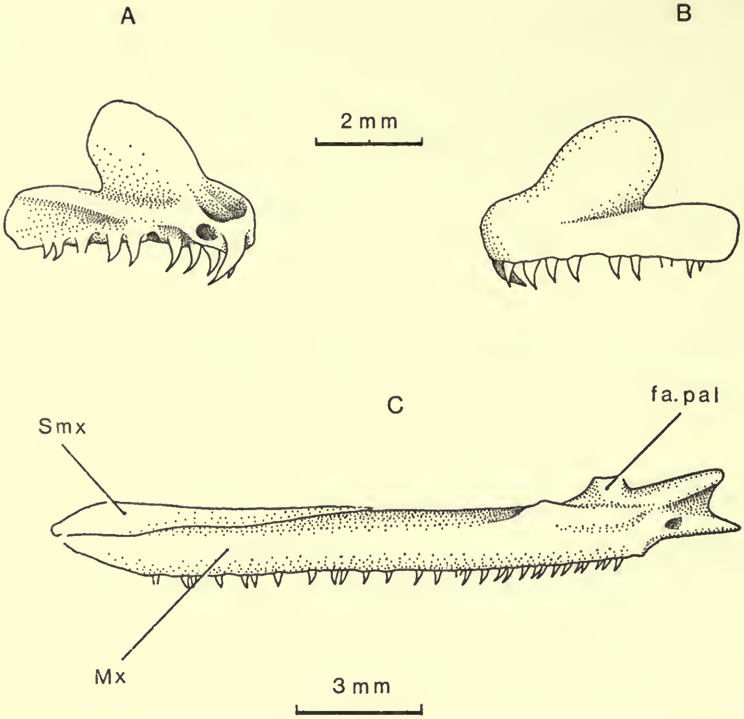

Fig. 17. *Rhacolepis buccalis* Agassiz. A: Left premaxilla in medial view. B: Left premaxilla in lateral view. Camera lucida drawings of isolated bone from UA 12026. C: Right maxilla and supramaxilla in lateral view.

inserted into this pocket. There are 10 marginal teeth, each distally recurved, the bases of which appear to be fused with the supporting bone. Additionally, there is one inner tooth at the anterior end of the premaxilla. It is considerably larger than a marginal tooth and is inclined almost horizontally. In most specimens examined there is a socket behind the inner tooth (Fig. 17A).

The maxilla (Fig. 17C, Mx) is elongate, with the head produced as two prongs joined by a bridge of thin bone. The ventral prong fits into the V-shaped groove of the premaxilla, making it unlikely that the premaxilla moved independently of the maxilla. A small, posteriorly directed fossa is present at the base of the ventral prong. This may have contained a ligament. There is no special facet developed for articulation with the ethmoid. The facet for articulation with the palatine (Fig. 17C, fa.pal) is well developed, and immediately behind this there is a low crest which may represent the point of insertion for a palatomaxillary ligament. There are approximately 35 teeth set in a single row on the maxilla. The teeth are slightly recurved and the bases appear fused with the supporting bone. A narrow ledge of bone lies lateral to the tooth base, thus in lateral view the true length of the tooth is not seen. In UA 12026 a maxilla 20 mm in length bears teeth 0·6 mm long. The supramaxilla (Fig. 17C, Smx) is represented by a thin splint half as long as the maxilla.

The lower jaw. The mandibular ramus is slightly longer than the upper jaw; it is generally shallow with a poorly-developed coronoid process. It differs from the lower jaw of *Notelops* in the fusion of elements posteriorly and in the dentition.

The dentary (Figs 11D, 19, Den) forms the major component of the mandibular ramus and overlaps the angulo-articular except at the coronoid process where the latter overlaps the former, a condition similar to that seen in *Notelops*. The lower margin of the dentary is slightly inflected. The dentary bears a single row of approximately 35 teeth, each of which is the same shape, but slightly larger than a maxillary tooth.

The angular and articular have fused together forming an angulo-articular (Fig. 11C, D, Ang-art). The articular portion, recognizable as a more ' spongy ' ossification, appears to form most of the articulatory facet (Fig. 11C, fa.qu). A well-developed postarticular process is present behind the articulatory facet. The posteroventral aspect of the angulo-articular is ornamented with ridges (Figs 11D, 19). The retroarticular (Figs 11C, 19, Rart) is a small ' hourglass-shaped ' element loosely connected to the inner surface of the angulo-articular, ventral and slightly posterior to the articulatory facet. It is often dissociated in acid-prepared specimens.

The mandibular sensory canal runs through the angulo-articular and the dentary. The canal opens to the lateral surface of the angulo-articular by three pores. In the dentary there are seven or eight short branches, each of which opens via a terminal pore. On the medial surface of the angulo-articular there is an anteriorly directed pore (seen in Fig. 11C) but it is uncertain if this led to the mandibular sensory canal.

Hyoid bar, urohyal, branchiostegal rays and gill arches. The ceratohyal is, as usual in lower teleosts, ossified in two sections representing anterior and posterior ceratohyals (Figs 18, 19, Ce.a, Ce.p), which were no doubt connected to one another by a cartilage-filled suture. The anterior ceratohyal is fenestrated and bears a deep lateral groove, and the posterior ceratohyal is grooved and sometimes fenestrated (Fig. 18). At the posterior end of the groove on the posterior ceratohyal there is a deeper pit which marks the point of origin of the hyoidean-mandibular ligament. There are two well-ossified hypohyals, the dorsal hypohyal slightly larger than the ventral. The interhyal is a small rod-like bone (Fig. 19, Int).

The exact number of branchiostegal rays is not known. Woodward (1887) records a count of twenty and this is probably a realistic estimate. There are approximately eight blade-like branchiostegal rays attached to the posterior ceratohyal. The anterior ceratohyal carries a series of approximately twelve fine rays which, as Woodward (1887) noted, are rather widely spaced.

The urohyal (Fig. 18, Ur) is long. Anteriorly it is rod-like. A cross-section through the posterior end would display an inverted V-shape with the tips of the limbs thickened.

The gill arches are reasonably well known from AMNH 4617, UA 12026 and particularly UA 12028 (Fig. 18). Most of the endochondral elements are ossified

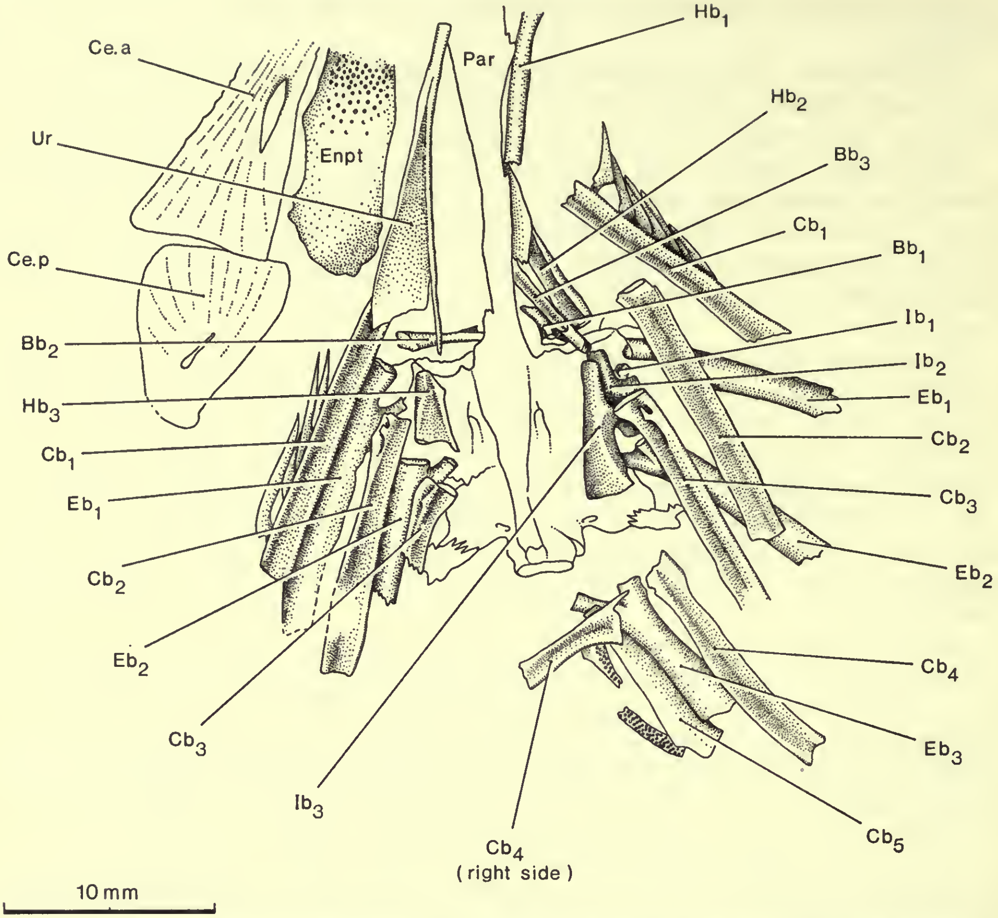

FIG. 18. *Rhacolepis buccalis* Agassiz. Camera lucida drawing of UA 12028 showing gill arches, braincase (in outline) and associated structures in ventral view.

and the membrane elements are separate from the endochondral elements over much of the series. The first, second and third basibranchials ($\mathrm{Bb}_{1, 2, 3}$) are ossified and support an elongate tooth plate (seen in AMNH 4617; Fig. 19, $\mathrm{Bb.tp}_{1+2+3}$) which represents a fusion of tooth plates associated with the first three basibranchials. In UA 12026 there is the suggestion that the tooth plate is fused with the third basibranchial but this could not be confirmed in any other specimen. No ossified basihyal or basihyal tooth plate could be identified. It is possible that the basibranchial tooth plate referred to above also incorporates a basihyal tooth plate since it is slightly longer than the combined length of the basibranchials.

The hypobranchials may be seen in Fig. 18; as usual in teleosts the first is the longest and the third is rather short and broader than the first two. The five ceratobranchials are unremarkable. There are four ossified epibranchials (Eb);

the fourth (not shown in figure) is deeply notched for the fourth efferent branchial artery. It may be noted that the dorsal ends of the first three epibranchials are more deeply forked than in *Elops*, but the significance of this difference is not clear to the author. The first infrapharyngobranchial (Ib_1) is a small element and articulates with the braincase immediately behind the foramen for the carotid artery. The second and third infrapharyngobranchials ($Ib_{2, 3}$) are larger and each bears a prominent process for articulation with the anterior epibranchial. In all, the second and third infrapharyngobranchials of *Rhacolepis* resemble those figured by Nelson (1968b : fig. 6B) for *Alepocephalus macropterus* more nearly than they do those of *Elops*.

The basibranchial tooth plate, described above, bears many small recurved teeth. Small, tooth-bearing plates are associated with the hypobranchials, ceratobranchials and epibranchials of the first two arches but their number and distribution could not

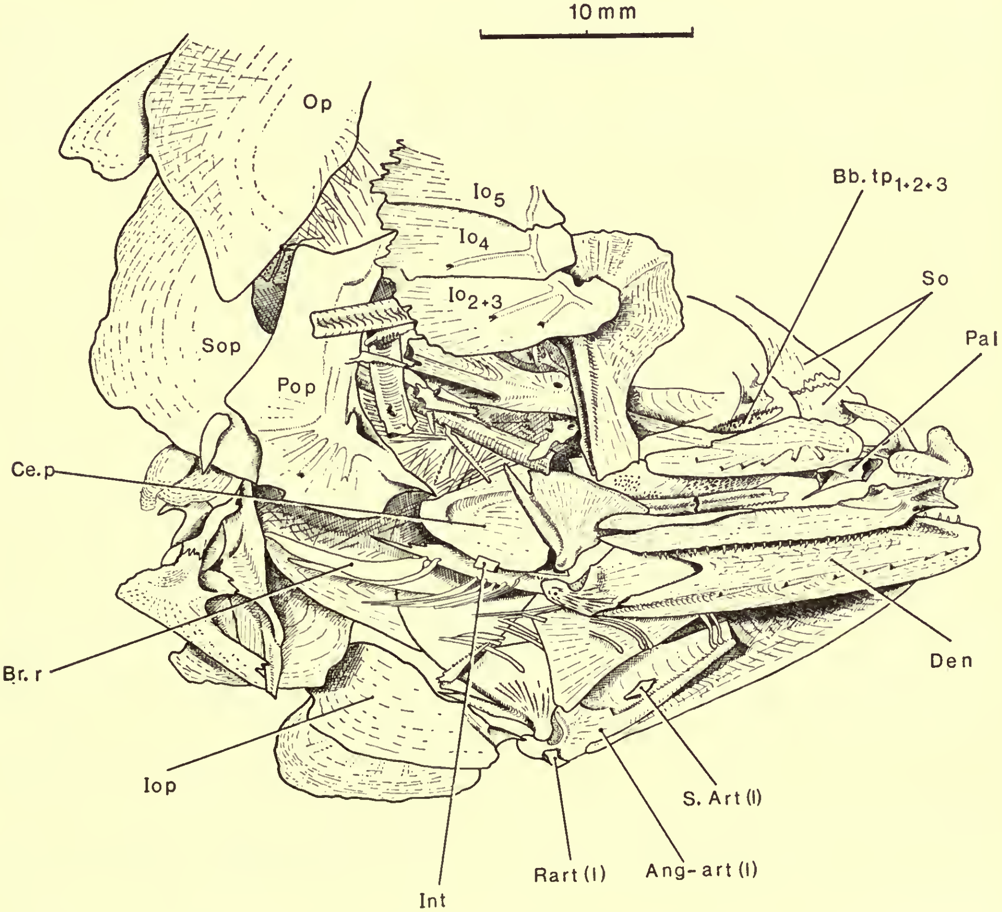

FIG. 19. *Rhacolepis buccalis* Agassiz. Camera lucida drawing of AMNH 4617.

be identified. The third epibranchial and the fifth ceratobranchial are also known to bear tooth plates. Upper pharyngeals could not be seen, but it is known (from UA 12028) that tooth plates are not fused with the second or third infrapharyngobranchials. Gill-rakers are present on the hypobranchials, ceratobranchials and epibranchials of the first two arches. They are quite long and bear many small teeth; their size and shape may be seen in Fig. 18. It is difficult to evaluate the information on the gill arch structure of *Rhacolepis buccalis*. In general terms the structure appears to be that expected in a primitive teleostean fish; most of the elements are present (a basihyal and suprapharyngobranchials were not seen), the tooth plates appear to be separate from the endochondral supports (with the possible exceptions noted) and there are no obviously specialized features. Furthermore, the gill arches cannot, at present, be compared to those of *Notelops* or *Pachyrhizodus* since the two latter are poorly known in this respect. The gill arches of *Rhacolepis buccalis* do not indicate any particular teleostean relationship.

Circumorbital series. The circumorbital series (Fig. 20) is composed of a supraorbital and five canal-bearing bones. The supraorbital (So) is narrow posteriorly where it is sutured with the dermosphenotic. It becomes broad anteroventrally where it abuts on the first infraorbital (Io_1). This latter element is elongate and rounded anteriorly, and meets the compound infraorbital behind in an oblique

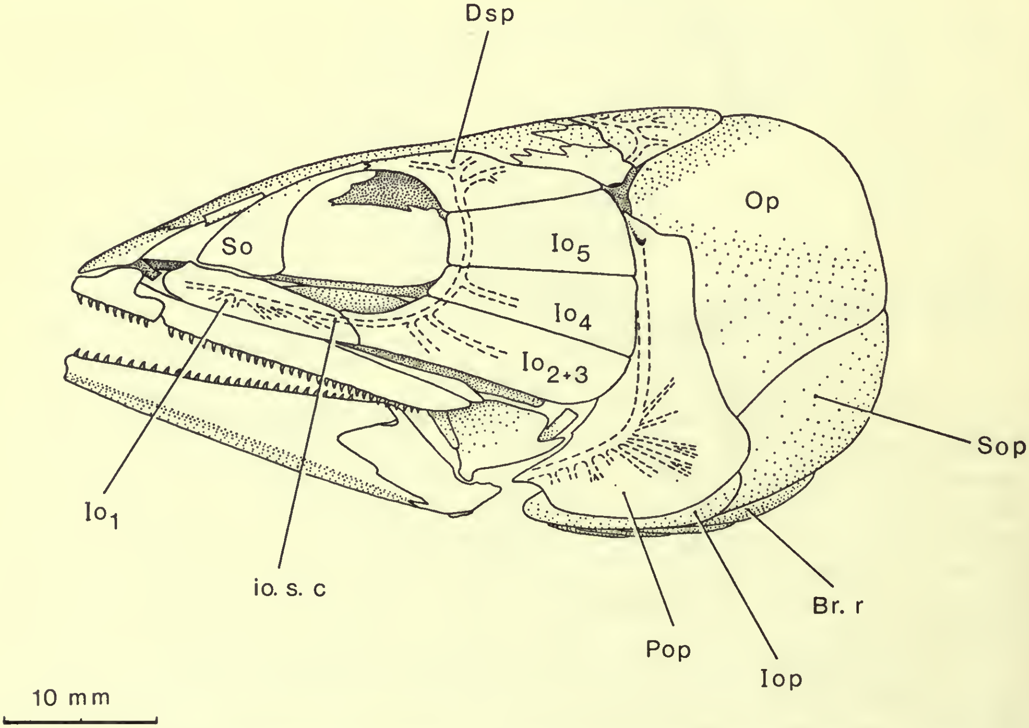

FIG. 20. *Rhacolepis buccalis* Agassiz. Restoration of cranium in left lateral view.

suture. The large infraorbital (Io_{2+3}) forming the posteroventral border to the orbit appears to represent the fused second and third infraorbitals of a primitive teleostean fish such as *Elops* (Nelson 1969). In this respect there is a resemblance to *Notelops*, but in that genus the infraorbital under discussion is deeper and carries three branches of the infraorbital sensory canal. The fourth (Io_4) and fifth (Io_5) infraorbitals are unfused (cf. *Notelops*) ; each is shallow but broad. The dermosphenotic (Dsp) or sixth infraorbital is large and completely covers the dilatator fossa as in *Pachyrhizodus megalops*. The dorsal margin of the dermosphenotic is contoured to fit the skull roof.

The infraorbital sensory canal (io.s.c) runs through the infraorbitals near the orbital margin. Five branches are given off in the first infraorbital, two in Io_{2+3} and one in the fourth infraorbital. Within the dermosphenotic the sensory canal splits into three branches, anterior, dorsal and posterior. The anterior branch is short but whether it opens terminally could not be ascertained. The posterior branch runs towards the frontal–pterotic contact and often bears a few ventral branches. There does not appear to be a connection between supraorbital and infraorbital sensory canals.

Opercular series. The opercular series is seen in Fig. 20. As in *Notelops* the operculum (Op) is large and dorsally is medially curved. The ventral margin is oblique and slightly concave. The suboperculum (Sop) is also relatively large. The preoperculum (Pop) differs from that of *Notelops* in being broader throughout and in having a better-developed ventral limb. The larger ventral limb in *Rhacolepis* may be due to the slightly more anterior position of the jaw articulation. Characteristically, the anteroventral margin of the preoperculum is excavated. The preopercular sensory canal runs away from the anterior margin at the base of the angle. The canal gives off approximately ten posterior/ventral branches, some of which may bifurcate. The interoperculum (Io) is broader (longer) than that element in *Notelops*.

Pectoral girdle and fin. The supratemporal (Fig. 12, Stt) is large and semicircular, as in *Notelops*. The supratemporal does not meet its partner in the midline, and if the supratemporal commissure was complete it must have run in the skin above the supraoccipital. The supratemporal commissure gives off three posterior branches within the supratemporal.

The post-temporal (Fig. 21A, Ptt) is relatively larger than that of *Notelops*, although of similar shape. The lateral line canal runs near the lateral margin. The supracleithrum (Fig. 21A, Scl) has a convex posterior margin and carries the continuation of the lateral line. There are several small posterior branches of the lateral line within the supracleithrum. The lateral line enters and leaves the supracleithrum lower down than in *Notelops*.

The cleithrum (Fig. 21A, Cl) is narrow and the dorsal limb is not as well developed as in *Notelops*. The posterior margin of the cleithrum is excavated at the fin insertion so that, in lateral view, part of the scapula and much of the coracoid may be seen. The cleithrum of *Notelops* is expanded at this level, covering both the scapula and fin insertion (Fig. 9). The scapula (Fig. 21A, Sca) completely encloses the scapular foramen and is produced posteriorly as a peg-like process. Both the

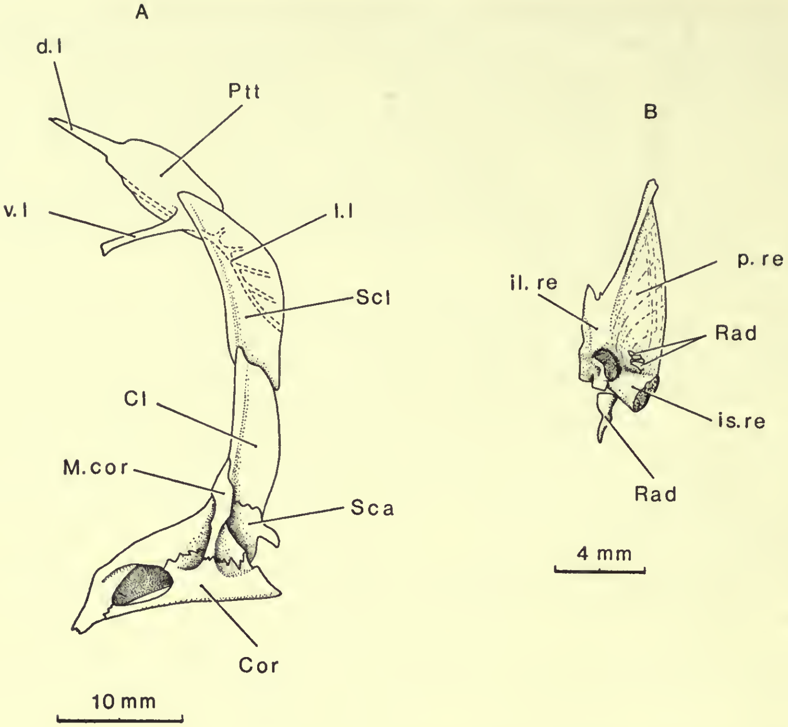

FIG. 21. *Rhacolepis buccalis* Agassiz. A: Restoration of right pectoral girdle in medial view. B: Left pelvic bone and radials in dorsal view. Camera lucida drawing of UA 12026.

mesocoracoid (Fig. 21A, M.cor) and the coracoid (Fig. 21A, Cor) are well developed. Between the cleithrum and the coracoid there is a large interosseus foramen. There are four proximal radials. The outermost is the shortest and has three articulating heads distally. The two outer radials articulate with the scapula, the inner two with the coracoid. The postcleithra are poorly known but there is sufficient evidence to suggest a similarity with those of *Notelops*.

The pectoral fin is held vertically and is composed of 16–17 rays. The outermost ray is unbranched and the second is the longest of the series, being equal in length to nine abdominal vertebrae. The fin is relatively much shorter than that of *Notelops*.

Pelvic girdle and fin. The pelvic fin originates behind the dorsal fin and is nearer to the caudal peduncle than to the pectoral fin. The fin is supported by a pelvic bone (Fig. 21B) which is more complex in shape than that of *Notelops*. The pelvic bone is thickened along the lateral and posterior margins. Between these thickenings there is a thin wing which is concave dorsally. The ischial region* is particularly thick and was presumably capped medially by cartilage. The iliac region bears two small articulatory facets along the posterior margin and a large articulatory facet dorsally and ventrally. Each of these facets was probably capped with cartilage. The large articulatory facets on the dorsal and ventral surface received the bases of the outermost one or two rays. The two posterior facets articulated with two small proximal radials. The third, innermost proximal radial is large and is produced as a spinous process but is not fused to any fin-ray. The iliac region bears a small anterior process that is separate from the main thickening in the pubic region. The pelvic bone thus shows a degree of anterior bifurcation but this is not as well developed as it is in cyprinoids or siluroids.

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* The tetrapod adjectives ischial, pubic and iliac are useful in descriptive morphology of the teleost pelvic girdle, but the usage is not meant to imply homology with those elements in the tetrapod girdle. This practice follows Weitzman (1967).

There are 10–11 pelvic fin-rays, the outermost the only unbranched member of the series. The fin is very short, the longest fin-ray (the outermost) being equal to the length of four caudal vertebrae. A pelvic splint bone was not seen.

Vertebral column. The exact number of vertebrae is unknown. Woodward (1887) states that there are approximately 20 caudal vertebrae and not less than 24 in the abdominal region. I agree that there are approximately 20 caudal vertebrae, but the abdominal region contains at least 35 ; the total number of vertebrae is between 55 and 65.

All centra are as deep as long, amphicoelous and pierced centrally by a large canal for the notochord. The centra are ornamented by a complex system of anastomosing ridges which impart a spongy appearance to some of the caudal centra.

The neural arches are autogenous throughout the abdominal region but are fused with the centra in the caudal region. Throughout most of the abdominal region epineurals are fused with the neural arches. In the posterior abdominal and caudal regions epineurals appear to be absent. At least the first 25 abdominal centra bear autogenous parapophyses, which are ovoid in shape. Behind this level, the parapophyses are fused with the centra and become longer, with a facet developed on the posterior face. The pleural ribs are narrow and slightly curved ; they only partially encircle the abdominal cavity, as is usual in fishes with a rounded body. Ribs are absent from the first centrum.

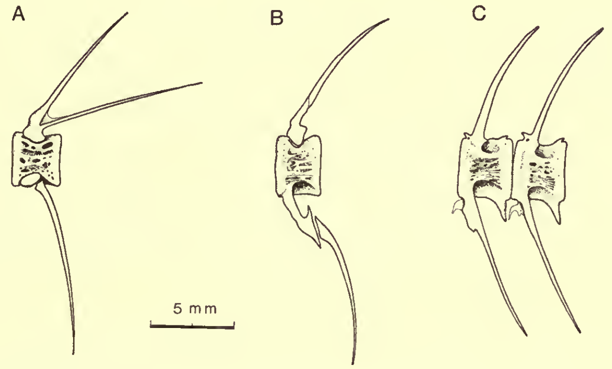

FIG. 22. *Rhacolepis buccalis* Agassiz. Vertebrae in left lateral view : A, from anterior abdominal region ; B, from posterior abdominal region ; C, from mid-caudal region.

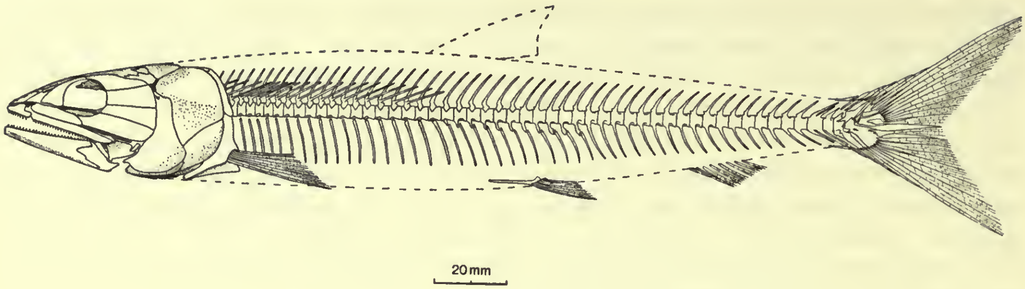

FIG. 23. *Rhacolepis buccalis* Agassiz. Entire fish, scales omitted.

The haemal arches are fused with the caudal centra. The neural and haemal arches of the caudal region bear anterior zygapophyses and there are also ventral posterior zygapophyses (Fig. 22C).

Dorsal and anal fins. The dorsal and anal fins are very poorly known. UA 12026 shows that the dorsal fin originates above the thirtieth vertebra which is probably located at the centre of the back (occiput-caudal peduncle). There are approximately 14 pterygiophores suggesting about 16 fin-rays. The first pterygiophore is distinctive in bearing a large membranous expansion. The base length of the dorsal fin is equal to the length of five and a half centra. The shape of the dorsal fin is unknown.

The anal fin is even more poorly known; it appears (UA 12027) to originate slightly nearer to the pelvics than the caudal peduncle. At least 7 fin-rays are present. Woodward (1887 : 538) suggests there are about 10 anal fin-rays.

Caudal skeleton and fin. The caudal fin-rays are supported by structures associated with two ural and three preural centra (Fig. 24A). The parhypural bears a small hypurapophysis but is otherwise similar to that seen in *Notelops*. The lower hypurals are fused (or partially fused) to one another and to the rather small first ural centrum (Fig. 24, $U_1+H_1+H_2$). At least two upper hypurals can be identified (Fig. 24B, H_3, H_4) H_3 being somewhat expanded distally. There are two uroneurals (Fig. 24, Un_1, Un_2), the first of which is deeply forked proximally and partially overlies the first preural centrum. The first uroneural also bears a small anterior projection. There are neural arches associated with the first and second preural centra, each fused to the supporting centrum. Two epurals are present. In three of four specimens in which the vertebrae in the caudal peduncle region were observed, the third preural centrum was seen to be a compound element (Fig. 24A, Pu_{3+4}) bearing two neural and haemal spines. The significance of this is not clear but similar 'double vertebrae', immediately in front of the caudal peduncle, are frequently seen in cyprinid caudal skeletons.

There are 19 principal fin-rays, the innermost of each lobe with expanded bases. Preceding the uppermost principal ray there are five procurrent rays and a dorsal caudal scute. Preceding the lowermost principal ray there are four procurrent rays and a ventral caudal scute.

Squamation. Cycloid scales cover the body and the bases of the caudal, dorsal and anal fins. The scales are thin and ovoid, being deeper than long. The scales covering the anterior part of the trunk are noticeably larger than those posteriorly. The dorsal and ventral fields are marked by evenly spaced circuli. In the anterior field the circuli break up into ridges without any definable pattern. The posterior field is marked by many fine, radiating ridges. Bone-cell spaces are present in the anterior field. In many specimens the scales are partially abraded and the posterior

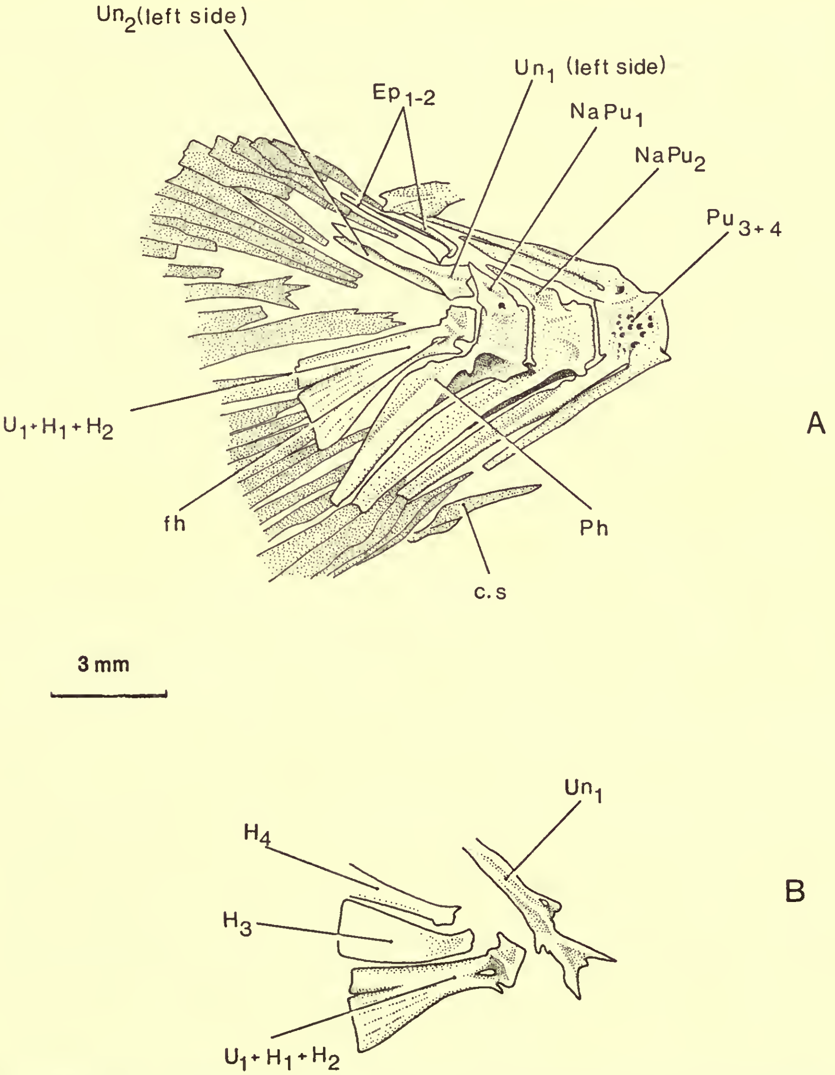

FIG. 24. *Rhacolepis buccalis* Agassiz. A : Caudal skeleton and fin in right lateral view. Camera lucida drawing of UA 12027. B : Uroneural and hypurals in right lateral view. Camera lucida drawing of UA 12026.

margins often have a crenulated appearance. Indeed, such a preservation led Agassiz (1844) to assign *Rhacolepis* (including *Notelops*) to his order Ctenoides.

A complete lateral line scale count could not be made but there are estimated to be about 90. The transverse count in front of the dorsal fin is about 10 above and about 11 below the lateral line row. The lateral line scales bear a tube, which is only seen in well-preserved specimens. A large, pointed pectoral axillary scale is present and above this, in the same transverse row, there is another large but less pointed scale.

Other species of Rhacolepis. Agassiz (1841 : 83) described *Rhacolepis latus* (generic name incorrectly spelled *Phacolepis*) from the same formation and locality as the type species. Woodward (1887 : 539 ; pl. 47, fig. 5) described this form more completely. The type specimen (BM(NH) P.1959) is distorted and there is some degree of post mortem anteroposterior compression, so that the true position of the fins is unknown. Jordan (1921 : 68) doubts the validity of this species. As can be seen from Woodward's figure the operculum is deep and shows a convex ventral margin, unlike *R. buccalis* but similar to *Brannerion vestitum.* The validity of this species must remain in doubt.

A third species, *Rhacolepis defiorei,* is described by d'Erasmo (1938), from the Santana Formation, Ceará, Brazil. I have not seen any of the material on which this species is based and do not therefore comment on its status. Santos & Valença (1968 : table 1) recognize all three species, *R. buccalis, R. latus* and *R. defiorei.*

Genus ***PACHYRHIZODUS*** Dixon 1850

1850 *Pachyrhizodus* Dixon : 374.
1872 *Thrissopater* Günther : 1.

DIAGNOSIS (emended). Pachyrhizodontid fishes in which the skull roof is marked with a frontal depression, dermethmoid broad, dilatator fossa with a roof posteriorly, pterotic not produced into a spine ; exoccipitals meeting above but not below foramen magnum, endochondral elements of the otic region of the braincase united by interdigitating sutures, no fenestra between autosphenotic and pterotic, foramen for the orbital artery and the posterior opening of the jugular canal close together on the lateral face of prootic and enclosed within a ' prootic cup ' ; anterior ceratohyal with or without fenestra ; posterior infraorbitals usually very broad, overlying preoperculum and often much of the operculum ; preoperculum expanded posteroventrally and with tapered vertical limb, preopercular sensory canal profusely branched, operculum with oblique ventral margin, interoperculum longer than deep ; ventral postcleithrum expanded posteriorly, outer pectoral fin-ray large and closely articulated ; caudal fin-rays (where known) crossing hypurals at a steep angle.

TYPE SPECIES. *Pachyrhizodus basalis* Dixon.

REMARKS. The two genera *Thrissopater* Günther and *Pachyrhizodus* Dixon are generally recognized as being very similar. Woodward (1901) in diagnosing them implied that they may be distinguished by two features : *Thrissopater* shows a frontal depression which is absent in *Pachyrhizodus* ; *Pachyrhizodus* bears an inner tooth on the premaxilla whereas there is no inner tooth in *Thrissopater.* Woodward (1908) later referred *Thrissopater magnus* Woodward to the genus *Pachyrhizodus* and stated that the latter genus does, in fact, exhibit a frontal depression. The only feature separating the two genera would seem to be the presence of an inner premaxillary tooth in *Pachyrhizodus.*

The presence or absence of an inner premaxillary tooth is very difficult to verify in the specimens referrable to *Thrissopater salmoneus* Günther and *Thrissopater megalops* Woodward. Specimens of *T. salmoneus* are poorly preserved in Gault Clay and those that show the premaxilla are not preparable. One specimen, BM(NH) 47199, does show a large tooth close to the imperfectly preserved premaxilla. This tooth has much the same form as the inner premaxillary tooth of *Pachyrhizodus subulidens* (Owen). No specimen of *Thrissopater megalops,* except the holotype, shows a premaxilla and consequently it is difficult to check the condition here. In view of the fact that *Thrissopater* and *Pachyrhizodus* are similar in all other cranial characters and there is no clear-cut difference between them, I propose to include *Thrissopater* within the genus *Pachyrhizodus.*

The following description is based upon *Pachyrhizodus megalops* (Woodward). The choice of this species, as representative of the genus, was governed by the availability of a cranium that could be prepared in acid. In some respects this choice is unfortunate since *P. megalops* is known to differ from other species in the large orbit and the differentiation of the teeth along the length of the jaws. However, the braincase and other cranial features of *P. megalops* agree closely with those of other English species represented by cranial material, *P. magnus* and *P. subulidens.*

Pachyrhizodus megalops (Woodward)

(Figs. 25–31)

1901 *Thrissopater megalops* Woodward : 35 ; pl. 7, fig. 4.
1908 *Thrissopater megalops* Woodward : 136 ; pl. 28, fig. 5.

DIAGNOSIS (emended). Small species of *Pachyrhizodus* in which the width of the skull roof at the level of the autosphenotic is equal to its width at the occiput ; diameter of the orbit equal to approximately 55 per cent of neurocranial length ; posterior infraorbitals narrow, not covering preoperculum ; marginal teeth on premaxilla (*c.* 6 mm long) three times as long as those on the maxilla ; anterior teeth on dentary as large as the premaxillary teeth, but decreasing in length posteriorly ; teeth straight ; premaxilla with approximately 10 marginal teeth ; maxilla with approximately 35 teeth ; dentary without inflected ventral margin.

HOLOTYPE. BM(NH) 49826, incomplete head, Lower Chalk (Zone of *Holaster subglobosus* – Upper Cenomanian), Sussex, England.

MATERIAL. The holotype and BM(NH) 16328 (prepared in acid), GSM temporary number (TN) 5738. The last-mentioned specimen is the property of the Dorking Museum but is retained in the Institute of Geological Sciences (Geological Survey Museum), London.

FORMATION AND LOCALITY. Lower Chalk (Cenomanian), Sussex, England.

DESCRIPTION. *Braincase.* The skull roof is broad, the greatest width, at the level of the autosphenotic spines, equal to half the length of the braincase. The braincase is deep, the maximum depth occurring at the angle of the parasphenoid and being nearly equal to half the braincase length. It is not known if all species of *Pachyrhizodus* have a deep neurocranium. *Pachyrhizodus megalops* has a large orbit (diameter equal to half the braincase length) and perhaps this causes the neurocranium to be deep (Forey 1973b : 66). Other English species of *Pachyrhizodus* have relatively smaller orbits.

The skull roof is flat above the orbit, raised at the centre of ossification of each frontal and markedly convex in the otic region. Although the extreme tip of the snout is missing in all specimens, it appears to have been rather blunt.

The dermethmoid (Fig. 25, De) is broad and is marked by fine ridges. The margin of the dermethmoid is poorly known. In ventral view (Fig. 29) the dermethmoid is raised into anteromedially directed ' tubes ', which make an impression on the dorsal surface anteriorly. There is no trace of an ethmoid commissure (cf. *Notelops*). The bone is very thin. In *P. megalops* there is no mesethmoid but in *P. subulidens* (Owen) the mesethmoid is a spongy ossification. The dermethmoid of the latter species is unknown.

The frontals form a very large proportion of the skull roof. They are medially united throughout their length by a suture which becomes sinuous in the epiphyseal region, as in *Rhacolepis*. At this level there is a shallow median depression and may also be a transverse ridge running between the centres of ossification of the frontals. In *P. salmoneus* (Günther) and *P. subulidens* this depression and the transverse ridges are particularly well developed. The depression is probably a growth phenomenon and of little taxonomic significance ; it may also be seen in large specimens of *Chanos* (Ridewood 1905 : fig. 140A).

Each frontal (Fig. 25, Fr) is broad above the orbit but becomes narrower posteriorly. The lateral margin is excavated above the autosphenotic spine and there is no roof over the dilatator fossa, a situation comparable to that seen in *Rhacolepis*. The frontal is marked by ridges which radiate from the raised centre of ossification. The ridges running toward the anterolateral limit of the frontal are particularly well developed. The supraorbital sensory canal runs within the most pronounced of these ridges and opens on to the surface above the lateral ethmoid. A nasal could not be identified. Posteriorly, the supraorbital sensory canal has two branches : one runs laterally from the centre of ossification and opens to the surface above the autosphenotic spine ; another runs back and opens immediately anterior to the frontal/parietal contact. It proved impossible to determine if there was a connection between the supraorbital and infraorbital canals. A few, small, medially directed branches occur in front of the centre of ossification of the frontal.

The parietal (Fig. 25, Pa) is small, considerably wider than long, and is separated from its partner by the supraoccipital (Figs 25, 27, Soc). The latter element is marked dorsally by radiating ridges. The supraoccipital crest is very small. The supratemporal sensory canal (Fig. 27, f.stt.com) ran transversely through the dorsal limit of the crest. Near the top of the crest there is a foramen (Fig. 27, f.p.f) on

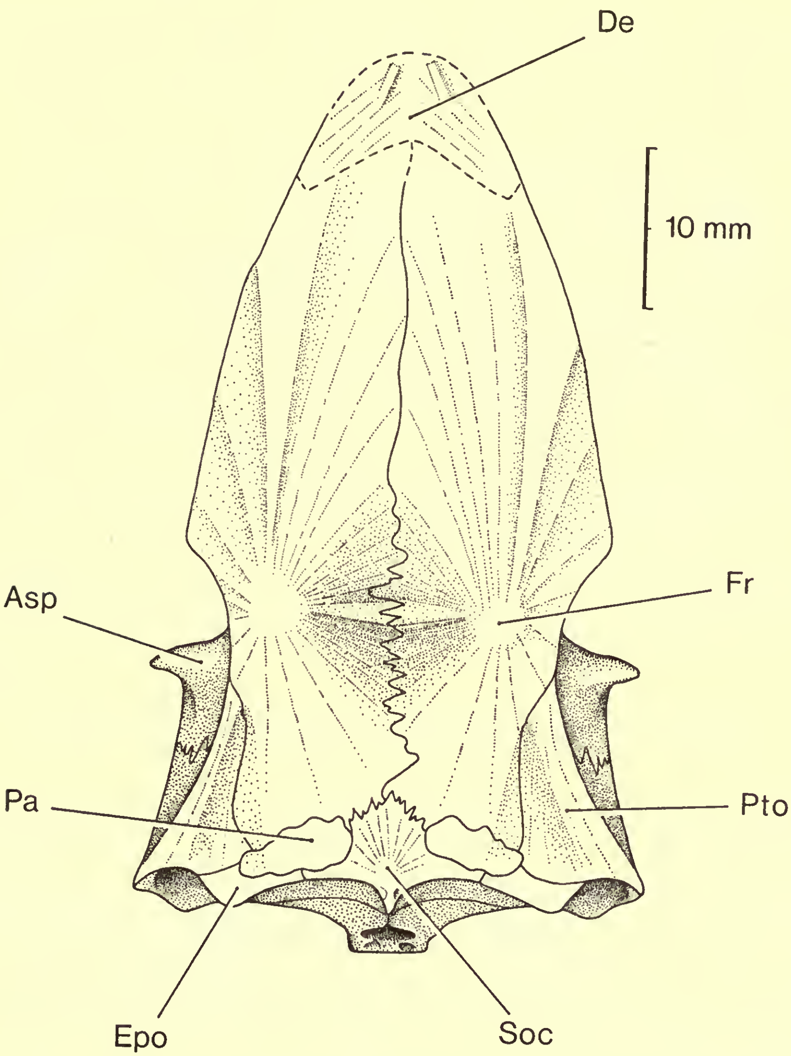

FIG. 25. *Pachyrhizodus megalops* (Woodward). Braincase in dorsal view. Based on BM(NH) P.16328.

either side of the midline, which leads from the posterior face of the braincase into the lumen of the post-temporal fossa. The function of this foramen is unknown ; its small size would suggest that it is not involved with musculature. It is possible that a tendon or nerve may have passed through here. A foramen in a similar position has been observed by Dr C. Patterson (personal communication), piercing the supraoccipital of *Rhacolepis*. I have also seen a foramen in the same position on one side of the supraoccipital crest of one specimen of *Notelops* (UA 12021). Below the skull roof the supraoccipital is produced as two anterolaterally directed

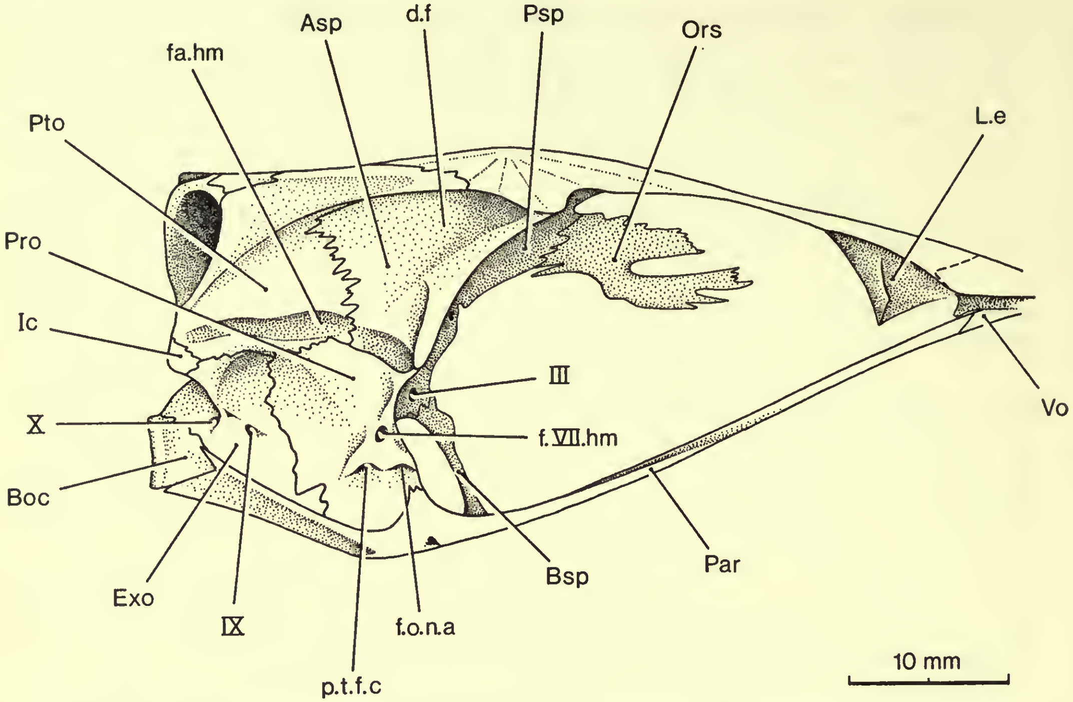

FIG. 26. *Pachyrhizodus megalops* (Woodward). Braincase in right lateral view. Based on BM(NH) P.16328.

wings. This results in a cup-shaped depression which is open anteriorly and covered by the frontals.

The epiotic (Figs 25, 27, Epo) is small and the epiotic process poorly developed. In the posterior view the epiotic may be seen to form the dorsomedial margin of the opening to the post-temporal fossa. This rim of the epiotic is thickened and suggests the usual course of the posterior semicircular canal through the epiotic.

The pterotic (Figs 25, 26, 27, Pto) forms the posterior half of the unroofed dilatator fossa and the greater proportion of the hyomandibular facet. The pterotic of *Pachyrhizodus megalops* is not produced as a posterior spine as it is in *Rhacolepis*. The dorsal surface of the pterotic bears a shallow groove, the inner areas of which continue on the frontal and parietal. A similar, but better-developed, groove is seen on the pterotic of *Esocelops cavifrons* Woodward. It is possible that a thin sliver of epaxial musculature lay in this groove. In posterior view the pterotic may be seen to form the lateral wall of the post-temporal fossa.

The intercalar (Figs 26, 27, Ic) is large and caps the junction between the epiotic, pterotic and exoccipital. Most of the intercalar is found on the posterior face of the neurocranium, where it forms part of the floor and the ventromedial margin of the opening to the post-temporal fossa. A prootic–intercalar bridge is absent.

The autosphenotic (Figs 25, 26, 28, 29, Asp) is large and bears a prominent autosphenotic spine, the true extent of which may only be seen in lateral view. The autospenotic forms much of the dilatator fossa, which is large in this species. The anterior third of the hyomandibular facet is formed by the autosphenotic. A foramen for the otic branch of the facial (Fig. 28, f.VII.ot) pierces the orbital face of the autosphenotic. The zigzag suture pattern between the autosphenotic and pterotic (Fig. 28) is more like that in *Rhacolepis* than *Notelops*. The inner surface of the autosphenotic forms the anterior wall of the post-temporal fossa.

The exoccipital (Figs 26, 29, Exo) meets its antimere above, but not below, the foramen magnum. The foramina for the vagus and glossopharyngeal nerves lay close together, as in *Rhacolepis*. The anterodorsal region of the lateral face of the exoccipital is concave, and with an adjacent concavity in the prootic forms a shallow depression in the position of a subtemporal fossa. The size of this depression does not merit the term ' fossa '. The basioccipital (Figs 26, 27, 29, Boc) is similar to that element in *Rhacolepis*. It is relatively small, and bears paired dorsal depressions suggesting that a neural arch articulated with the basioccipital. The basioccipital forms part of the foramen magnum.

The prootic (Figs 26, 28, 29, Pro) also bears certain resemblances to the prootic of *Rhacolepis*, in that the foramen for the trigeminal (Fig. 28, V) is separate from the anterior opening of the jugular canal (Fig. 28, a.t.f.c). The foramen for the occulomotor (Fig. 28, III) is situated medial to the trigeminal foramen (a slight difference from the condition in *Rhacolepis*, p. 150) and a separate foramen for the profundus

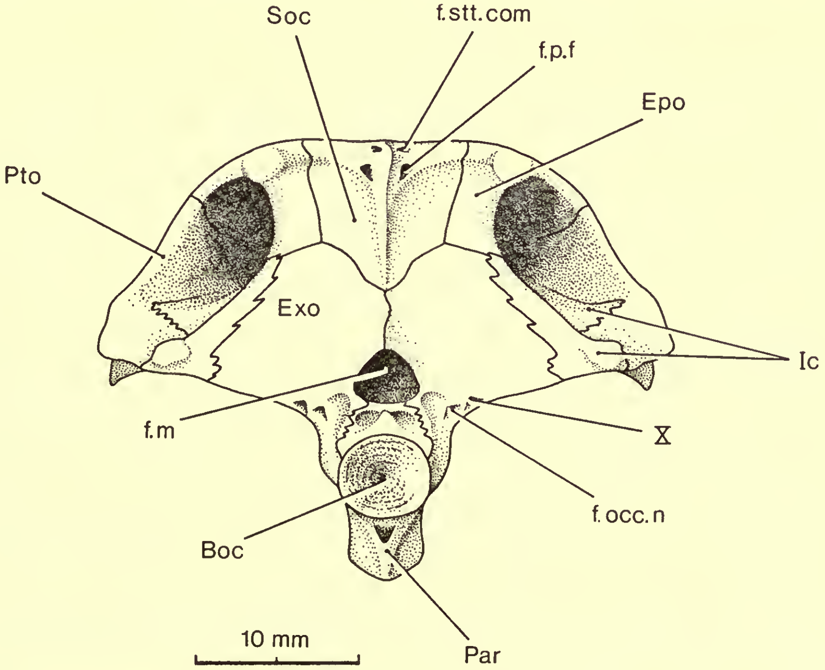

FIG. 27. *Pachyrhizodus megalops* (Woodward). Braincase in posterior view. Based on BM(NH) P.16328.

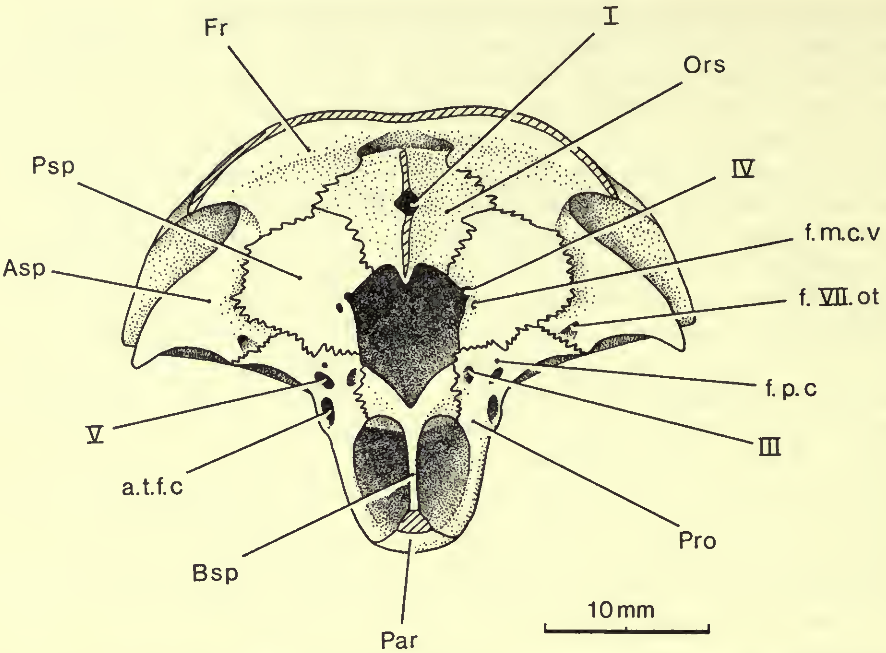

FIG. 28. *Pachyrhizodus megalops* (Woodward). Postorbital parts of the braincase in anterior view. Based on BM(NH) P.16328.

ciliaris (Fig. 28, f.p.c) is located above the trigeminal foramen. The lateral face of the prootic is different from that of *Rhacolepis* and *Notelops*. The foramen for the hyomandibular branch of the facial (Fig. 26, f.VII.hm) is situated in the lateral wall of the jugular canal. From the point of exit the hyomandibular branch ran dorsally in a deep groove on the prootic before turning posteriorly and laterally to pierce the medial face of the hyomandibular. The posterior opening of the jugular canal (Figs 26, 29, p.t.f.c) and the foramen for the orbital artery (Figs 26, 29, f.o.n.a) are very close together. Both of these ventral openings are embraced by a ridge of bone resulting in a cup-shaped structure, here termed the prootic cup. In *Rhacolepis* there is a ridge of bone connecting the widely separated openings of the jugular canal and the arterial foramen. In comparison with *Rhacolepis* the opening of the jugular canal in *P. megalops* has ‘ moved ’ anteroventrally and the connecting ridge has become shorter. In ventral view (Fig. 29) a small foramen may be seen opening into the anterior end of the prootic cup. This foramen leads into a short canal which joins with the canal for the orbital artery. It is possible that this small foramen was occupied by a posterior palatine branch of the facial. A prootic cup can be identified in *P. magnus* and is probably a generic character. The suture lines between the prootic and the adjacent exoccipital, autosphenotic, parasphenoid and basisphenoid are zigzag in shape.

The pterosphenoid (Figs 26, 28, 29, Psp) lies dorsal to the anterior (orbital) face of the prootic. The inner margin of the pterosphenoid forms part of the wall of the optic foramen. The inner margin is excavated for the passage of the trochlear (as in *Rhacolepis*) and there is a small foramen for the middle cerebral vein. The sutures between the pterosphenoid and neighbouring bones are of a complex zigzag form. The suture between the pterosphenoid and autosphenotic is rather unusual, the surface of the pterosphenoid being raised with respect to the autosphenotic.

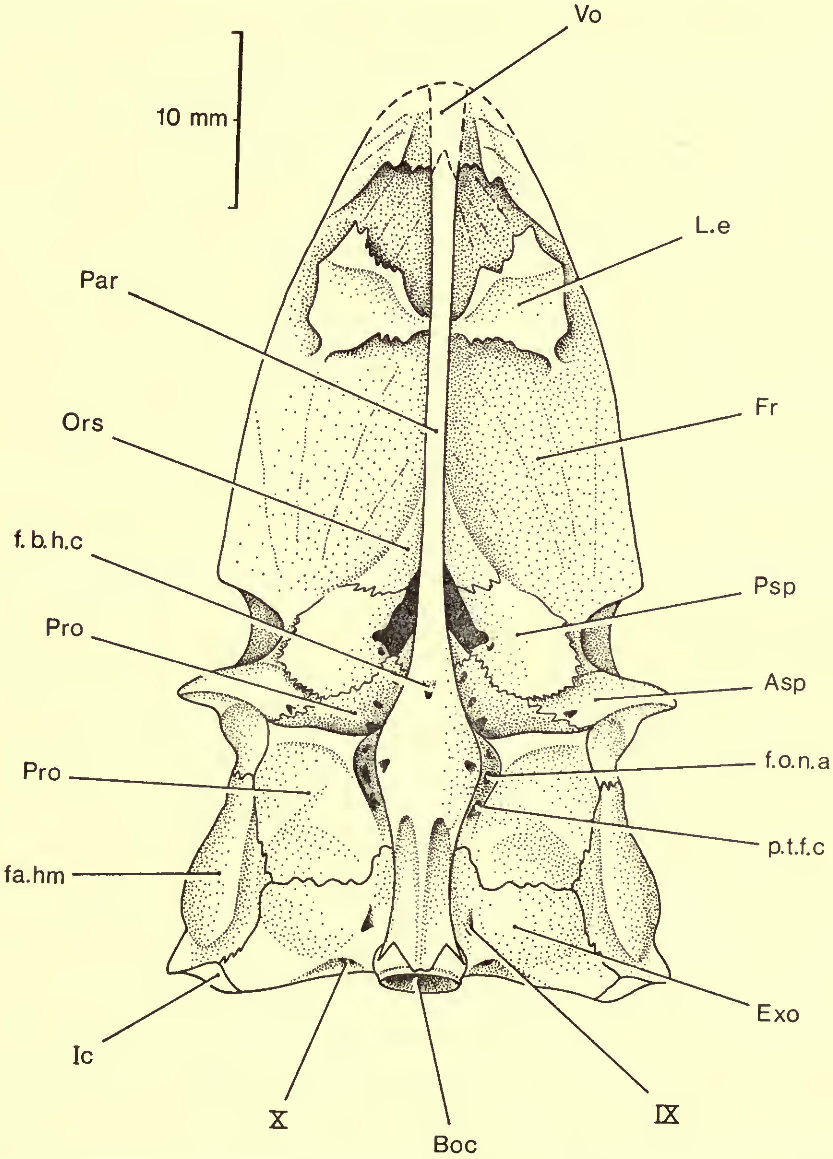
Vo
10 mm
L.e
Par
Fr
Ors
f.b.h.c
Psp
Pro
Asp
Pro
f.o.n.a
p.t.f.c
fa.hm
Exo
Ic
X
Boc
IX

FIG. 29. *Pachyrhizodus megalops* (Woodward). Braincase in ventral view. Based on BM(NH) P.16328.

This results in a groove which follows this suture and marks the path of the superficial ophthalmic branches of the trigeminal and facial.

The orbitosphenoid (Figs 26, 28, 29, Ors) forms the dorsal margin of the optic foramen and meets ventral flanges of the frontals dorsally and the pterosphenoids laterally. The olfactory tracts passed out through a deep excavation in the orbitosphenoid. The basisphenoid (Figs 26, 28, Bsp) forms the ventral margin of the optic foramen and is produced ventrally as a slender pedicel to contact the parasphenoid.

The parasphenoid (Figs 26, 27, 28, 29, Par) is long and angled beneath the prootic cup. Beneath the orbit the parasphenoid is narrow. The ascending wings are poorly developed. Posteriorly the parasphenoid becomes deeper and is marked by a groove on either side. There is a small posterior opening to the myodome, which lies between the parasphenoid and the basioccipital. This may be seen in Fig. 27. At the level of the ascending wing there is a foramen for the internal carotid artery and beneath the basisphenoid insertion there is a median foramen for the bucco-hypophyseal canal (Fig. 29, f.b.h.c). In all, the parasphenoid of *P. megalops* is very similar to that of *Rhacolepis*. The vomer (Figs 26, 29, Vo) is small but the precise limits of this element are unknown. The lateral ethmoid (Figs 26, 29, L.e) is represented by perichondral bone. Dorsally the lateral ethmoid contacts the frontals by a very narrow pedicel. Ventrally the lateral ethmoid expands in both transverse and parasagittal planes. No foramen in the transverse wall could be seen ; the olfactory tract and nasal artery presumably passed through cartilage medial to the lateral ethmoid.

Dermal upper jaw. The upper jaw is long and reaches back to a level beneath the posterior limit of the orbit. The jaw is formed by the premaxilla, maxilla and

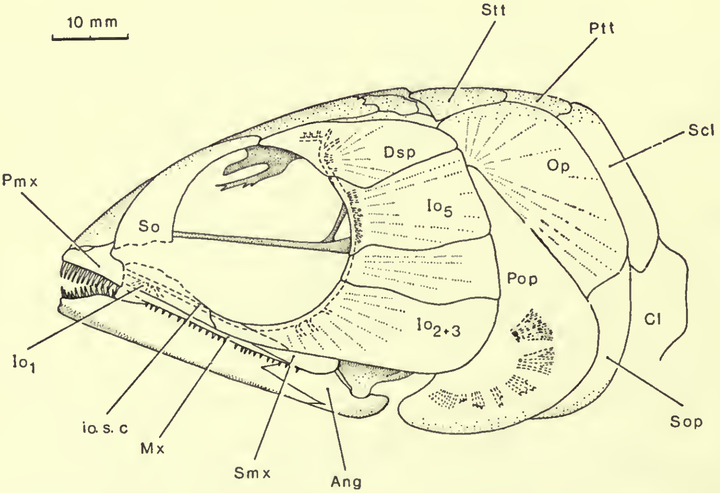

FIG. 30. *Pachyrhizodus megalops* (Woodward). Restoration of cranium in left lateral view.

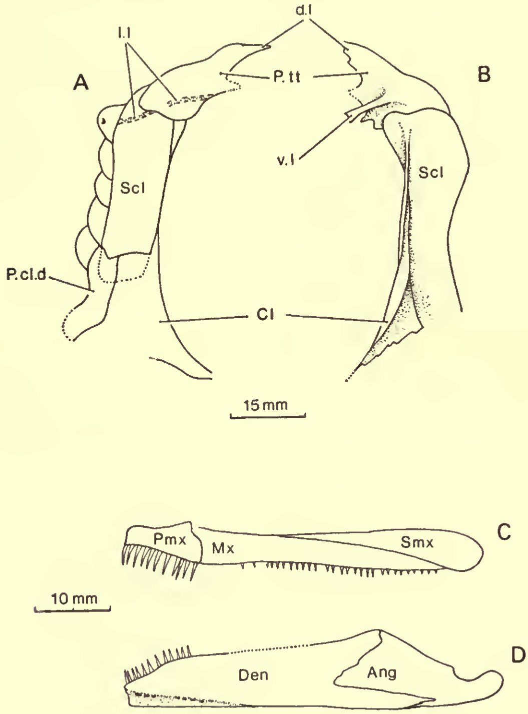

FIG. 31. *Pachyrhizodus megalops* (Woodward). A, B: Restoration of upper part of right pectoral girdle in lateral and medial views. C: Restoration of left upper jaw in lateral view. D: Restoration of left lower jaw in lateral view.

a single supramaxilla. The premaxilla (Fig. 30, Pmx) is small, equivalent in length to one-fifth of the total length of the upper jaw. The premaxilla is narrow anteriorly where it contacts its partner in the midline but becomes deeper posteriorly where it overlaps the head of the maxilla. A dorsal process on the premaxilla fits tightly against the dermethmoid. There are 9–11 long, needle-like premaxillary teeth.

The maxilla (Fig. 30, Mx) is long and shallow and fits tightly against the premaxilla anteriorly. Although the morphology of the premaxillary/maxillary overlap is not known in *P. megalops* I suspect it is similar to that seen in *P. subulidens* which is described below (p. 173). There are approximately 35 maxillary teeth set in a single row. Each maxillary tooth is less than half the length of a premaxillary tooth and is slightly stouter. As in *Notelops* and *Rhacolepis* there is a narrow ledge of bone lateral to the bases of the maxillary teeth.

Lower jaw. This is poorly known; it is only partly seen in lateral view in the specimens examined. The dentary (Fig. 31, Den) occupies nearly two-thirds of the lower jaw length. The anterior end of the dentary is truncated at the symphysis, from which the oral margin curves upwards for a distance before levelling off and passing backwards to the weakly-defined coronoid process. In the holotype there are 12 needle-like teeth in the anterior third of the oral margin of the dentary. An entire oral margin was not seen in any dentary so it is not known whether the tooth row extended back to the coronoid process. However, there are a few small teeth immediately anterior to the coronoid process in GSM (TN) 5738. The ventrolateral margin of the dentary is grooved. Within this groove, at the anterior end of the dentary, there are seven pores marking the path of the mandibular sensory canal.

The lateral face of the posterior third of the lower jaw is formed by the angular (Fig. 31, Ang). However, the medial aspect of the jaw is not known and therefore it is possible this bone should be termed an angulo-articular. The angular forms the lateral part of the articulating cup and is produced posteriorly as a retroarticular process.

Circumorbital series. This is composed of six (possibly seven) bones and completely surrounds the orbit. The supraorbital (Fig. 30, So) is very large, contacting the dermosphenotic posteriorly and curving anteroventrally to the tip of the premaxilla. The supraorbital lies tightly against the underlying lateral ethmoid.

The first infraorbital (Fig. 30, Io_1) is imperfectly displayed in GSM (TN) 5738. It is slightly expanded anteriorly and meets the infraorbital behind in an oblique suture. The presence of a second infraorbital cannot be demonstrated with confidence ; it could well be fused with the third infraorbital, as it appears to be in *Notelops* and *Rhacolepis*. The third infraorbital (Fig. 30, Io_{2+3}) is, as usual in many lower teleosts, a large element forming the posteroventral margin of the orbit. The fourth and fifth (Fig. 30, Io_5) are rectangular, being broader than deep. The dermosphenotic (Fig. 30, Dsp) is large and triangular and completely covers the dilatator fossa, as in *Rhacolepis*.

The infraorbital sensory canal runs at the orbital margin for much of its length. Anteriorly the sensory canal runs through the centre of the first infraorbital and gives off four ventral branches. Within the third infraorbital there are three branches, while in the fifth infraorbital there are many branches but not all of these open to the surface. Within the dermosphenotic the main sensory canal runs dorsally and gives off a blindly-ending anterior branch and a posterior branch which opens to the surface. There are also several smaller branches which may be seen in Fig. 30. The infraorbital sensory canal of *P. megalops* is remarkable for the prolific branching in the dermosphenotic and the fifth infraorbital.

Opercular series. Compared to *Rhacolepis*, the operculum (Fig. 30, Op) of *P. megalops* is narrow and the preoperculum (Fig. 30, Pop) overlaps much of the operculum and suboperculum. The preopercular sensory canal is (like the infraorbital canal) profusely branched. These branches are arranged in six groups (Fig. 30) in BM(NH) P.10219 ; they are more evenly arranged in GSM (TN) 5738. An interoperculum was not seen in *P. megalops*.

Postcranial skeleton. Little is known of the postcranial skeleton. One specimen, GSM (TN) 5738, shows a few vertebrae. The ornamentation of the centra is confined to a few longitudinal grooves. In this *P. megalops* is similar to other smaller species such as *P. salmoneus* (Günther) and *P. subulidens* (Owen) but different from larger species such as *P. dibleyi* Woodward and *P. basalis* Dixon in which the surface of the vertebrae is smooth.

Of the shoulder girdle, the post-temporal, supracleithrum and part of the cleithrum are known in *P. megalops*. Significant points are the broad post-temporal and the spine-like tip of the cleithrum which reaches well up the medial surface of the supracleithrum (Fig. 31B). Neither of these features is seen in *Notelops* nor *Rhacolepis*. The only part of the pectoral fin known is the outer ray. It is stout and closely articulated. The holotype of *P. salmoneus* shows a similar stout outer pectoral fin-ray.

Squamation. The scales of *P. megalops* are cycloid, almost circular and 5–6 mm in diameter. The anterior and lateral fields are marked by fine, evenly-spaced circuli. The posterior field is marked by small tuberculations which are arranged to give the appearance of fine, longitudinal ridges.

Other English species of *Pachyrhizodus*

Woodward (1907, 1908) describes material of *Pachyrhizodus* (and *Thrissopater*) from the English Chalk. The following notes supplement that work.

In addition to *P. megalops* two further species of the genus are reasonably well known from cranial remains, *P. subulidens* (Owen) and *P. magnus* (Woodward). Both exhibit a skull roof that is similar to that of *P. megalops*. In *P. subulidens* (Woodward 1908 : fig. 39 ; pl. 27, fig. 1a) the frontals above the orbit and the dermethmoid are particularly broad and the depressions on the skull roof are large. In both species the dilatator fossa is more extensively roofed than in *P. megalops* and the parietals are relatively smaller. The circumorbital series is similar to that of *P. megalops* in being composed of a large supraorbital (antorbital of Woodward 1908) followed by five infraorbitals. However, the orbit is smaller and the posterior infraorbitals are very broad and become very thin at their posterior margins. In *P. subulidens* the preoperculum is expanded posteroventrally and, with the large posterior infraorbitals, virtually covers the operculum and suboperculum.

The premaxilla of *P. magnus* (Woodward 1908 ; pl. 28, fig. 1) is deeper than in *P. megalops* and the dorsal process is better developed. The premaxillae of the larger species (*P. basalis* Dixon and *P. dibleyi* Woodward) are not found associated, but the angle of tooth implantation shows that the outer surface of the premaxilla must have been held almost horizontally. The premaxilla/maxilla overlap is known in *P. subulidens* (Fig. 32). The premaxilla fits into a shallow notch in the lateral face of the maxilla. The medial surface of the premaxilla has a well-developed ridge fitting into this notch. This premaxilla/maxilla overlap must limit independent movement between these bones. Anteriorly, there is a small facet (Fig. 32, fa.eth) for articulation with the ethmoid ; in this species there is a small mesethmoid.

The morphology of the mandibular ramus varies between the different species, the chief variation being in the dentition (see diagnoses). It is of interest to note that in *P. sublidens* and *P. magnus*, in which complete rami are known, the lateral expression of the angular (? angulo-articular) is very small compared to that of the dentary. This is also observed in *Notelops* and *Rhacolepis*. The dentary of the larger species (*P. basalis* and *P. subulidens*) shows a strongly inflected ventral margin, not seen in *P. megalops*.

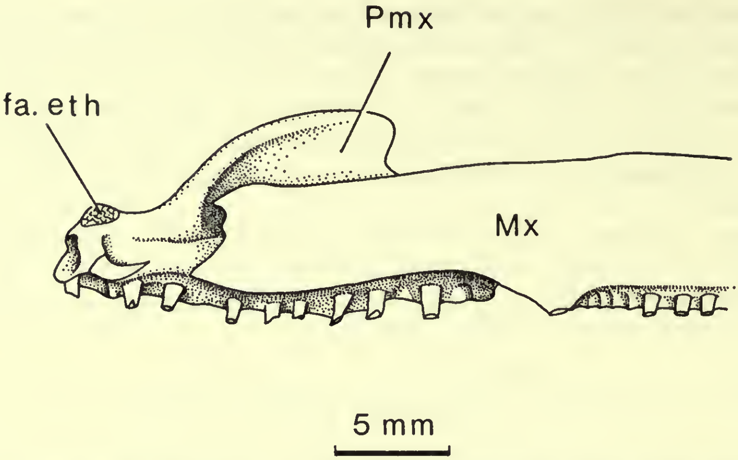

Fig. 32. *Pachyrhizodus subulidens* (Owen). Freehand sketch of right premaxilla and head of maxilla in medial view. Based on BM(NH) P.4298.

The caudal skeleton and fin of the English species of *Pachyrhizodus* are very poorly known. Woodward (1907 : 124 ; pl. 26, fig. 6) suggested that BM(NH) P.5659, a specimen showing a posterior caudal region and caudal fin, is referable to *Pachyrhizodus*. The identity of this specimen is still in doubt and unfortunately the details of the endoskeleton are too poor to allow a critical assessment. However, the caudal fin-rays are closely segmented nearly to their bases. This feature is noted in *P. caninus* (Hay 1903 : pl. 3). The holotype of *P. salmoneus* and an unregistered specimen of *P. subulidens* in the Sedgwick Museum, Cambridge, each show a small part of the caudal skeleton. In both the base of the first uroneural is much expanded and covers much of the first and second preural centra. These specimens also show that the upper principal fin-rays cross the fused upper hypurals at a steep angle.

There are many specimens (mostly jaw fragments) from the English Chalk which can be referred to the genus *Pachyrhizodus* and it seems worth while to attempt rediagnoses of the species. Details of jaw features are emphasized in so doing.

Pachyrhizodus salmoneus (Günther)

1872 *Thrissopater salmoneus* Günther : pl. 1.
1901 *Thrissopater salmoneus* Günther ; Woodward : 33.

Diagnosis (emended). Small species of *Pachyrhizodus* in which the width of the skull roof at the level of the autosphenotic is considerably less than the width of the skull roof at the occiput ; diameter of the orbit equal to approximately 25 per cent of neurocranial length ; posterior infraorbitals broad, covering much of the preoperculum ; marginal teeth on premaxilla, teeth on maxilla and dentary of equal size (1–1·5 mm long) and slightly curved, premaxilla with approximately 10 marginal teeth and a single, large, straight inner tooth, maxilla with approximately 40 teeth ;

dentary without strongly inflected ventral margin; approximately 50 vertebrae, marked by numerous fine ridges; scales small (*c.* 5 mm deep), not less than 35 in a transverse series anterior to the dorsal fin.

HOLOTYPE. SMB 42459, incomplete fish, Gault Clay (Albian) of Folkestone, Kent, England.

MATERIAL. The holotype and BM(NH) 47194, 47197, 47198, 47199, 47202, P.16, P.41, P.9999 (2 specimens).

FORMATION AND LOCALITY. Gault Clay (Albian), Kent, England.

Pachyrhizodus magnus (Woodward)

1837 *Hypsodon lewesiensis* Agassiz : pl. 25a, fig. 1; pl. 25b, figs 4, 5 (errore).
1844 *Hypsodon lewesiensis* Agassiz **5** (1) : 100.
1901 *Thrissopater magnus* Woodward : 33; pl. 5, figs 1, 2.
1908 *Pachyrhizodus*(?) *magnus* (Woodward); Woodward : 131; pl. 28, fig. 1.

DIAGNOSIS (emended). Small species of *Pachyrhizodus* in which the width of the skull roof at the autosphenotics is nearly equal to its width at the occiput; diameter of the orbit equal to approximately 30 per cent of neurocranial length; posterior infraorbitals broad, covering much of preoperculum; marginal teeth on premaxilla and teeth on maxilla and dentary of equal or nearly equal size (1·5–2 mm long), teeth straight, premaxilla with approximately 14 marginal teeth and a single inner tooth which is only slightly larger than the marginal teeth, maxilla with approximately 40 teeth, dentary without strongly inflected ventral margin; vertebrae marked by a few small pits.

HOLOTYPE. BM(NH) 37981, incomplete head from Lower Chalk (probably Zone of *Holaster subglobosus* – Upper Cenomanian) of Kent, England.

MATERIAL. Only the holotype is known.

Pachyrhizodus subulidens (Owen)

(Fig. 32)

1840 *Raphiosaurus subulidens* Owen : 190.
1850 *Raphiosaurus lucius* Owen; Dixon : 385; pl. 39, figs 1–3.
1851 *Raphiosaurus subulidens* Owen : 19; pl. 10, figs 5, 6.
1889 *Pachyrhizodus subulidens* (Owen); Woodward : 351.
1901 *Pachyrhizodus subulidens* (Owen); Woodward : 43; pl. 7, figs 1, 2; pl. 5, fig. 2.
1908 *Pachyrhizodus subulidens* (Owen); Woodward : 129, fig. 39; pl. 27, figs 1–4.
? 1911 *Pachyrhizodus* sp. Woodward : 249; pl. 54, figs 2.

DIAGNOSIS (emended). Small species of *Pachyrhizodus* in which the width of the skull roof at the autosphenotic is nearly equal to its width at the occiput; diameter of the orbit equal to approximately 30 per cent of neurocranial length; posterior infraorbitals broad, covering much of the preoperculum; marginal teeth on premaxilla and teeth on maxilla of equal size (3–4 mm long), teeth on dentary much larger (6–7 mm long), all teeth on dermal jaw bones recurved, premaxilla with approximately 10 marginal teeth and a single inner tooth which is only slightly larger than the marginal teeth, maxilla with 30–40 sockets, dentary with not less than 30 sockets ; dentary with inflected ventral margin, the width of which does not exceed the depth of the dentary.

HOLOTYPE. SM B.9097, portion of maxilla from Lower Chalk (Zone of *Holaster subglobosus* – Upper Cenomanian), Cambridgeshire, England.

MATERIAL. The holotype, also SM B.94762a–c, B.94762d–j, B.94557, and BM(NH) 36635, 38566, 39079, 49078, P.1808, P.4298, P.6527, P.10812, P.11802, P.12896. The following are probably specimens of this species : BM(NH) 36138, 39087, P.4299.

FORMATION AND LOCALITY. Lower Chalk (Cenomanian), Cambridgeshire, Sussex and Kent, England.

Pachyrhizodus basalis Dixon

1837 *Hypsodon lewesiensis* Agassiz : pl. 25a, figs 2, 4 ; pl. 25b, figs 4–7.
1844 *Hypsodon lewesiensis* Agassiz **5** (1) : 99.
1850 *Pachyrhizodus basalis* Dixon : 374 ; pl. 34, figs 9, 10.
1869 *Acrodontosaurus gardneri* Mason : 444 ; pl. 19.
1877 *Hypsodon lewesiensis* Agassiz ; Newton : 508.
1888 *Pachyrhizodus gardneri* (Mason) ; Woodward : 314.
1901 *Pachyrhizodus basalis* Dixon ; Woodward : 37.
1901 *Pachyrhizodus gardneri* (Mason) ; Woodward : 40.
1907 *Pachyrhizodus basalis* Dixon ; Woodward : 125 ; pl. 25, figs 1, 2.
1907 *Pachyrhizodus gardneri* (Mason) ; Woodward : 125 ; pl. 25, figs 3–8 ; pl. 26, fig. 5.

DIAGNOSIS (emended). Large species of *Pachyrhizodus* in which the marginal teeth on the premaxilla are slightly larger than those on the maxilla, teeth on dentary larger than those on the upper jaw, marginal teeth on premaxilla and teeth on maxilla and dentary recurved, premaxilla with approximately 9 marginal teeth and one or two large inner teeth that may be slightly recurved or straight, dentary with 25–30 tooth sockets ; dentary with strongly inflected vental margin, the width of which exceeds the depth of the dentary.

HOLOTYPE. BM(NH) 49014, right maxilla, Lower Chalk (probably Zone of *Holaster subglobosus* – Upper Cenomanian) of Kent, England.

MATERIAL. The holotype, also SM B.94556 and BM(NH) 4105, 25791, 25792, 33256, 33257, 41671, 41674, 47236, 49757, 49905, P.5655, P.5656, P.9016, P.9697, P.10031, P.10044, P.11009, P.11908, P.12353, P.12892. The following are probably specimens of this species : SM B.40859, B.40860, B.40861, B.94555 and BM(NH) 4068, P.1808a, P.4506, P.5652, P.5653, P.5658.

FORMATIONS AND LOCALITIES. The majority of specimens are from the Lower Chalk (Cenomanian) of Surrey, Kent and Sussex, England. BM(NH) 4068 and 4105 are from the Middle Chalk (Zone of *Terebratulina lata* – Turonian) of Sussex, England. Woodward (1907 : 128) notes that specimens are recorded from Upper Chalk (Zone of *Micraster coranguinum* – Santonian) of Surrey, England, but this could not be verified.

Remarks. Woodward (1901, 1907) recognized two species, *P. basalis* Dixon and *P. gardneri* (Mason), which are here placed in synonymy under the prior name *P. basalis*. Woodward maintained that in *P. gardneri* the base of the inner premaxillary tooth reaches to the inner margin of the premaxilla and the tooth shows a slight inward curvature, while in *P. basalis* the inner premaxillary teeth are straight and the teeth bases stand away from the inner margin of the premaxilla. An examination of specimens referred to the two species shows that these features are within the limits of individual variation. In the absence of more complete material these species should therefore be considered synonymous.

Pachyrhizodus dibleyi Woodward

1901 *Pachyrhizodus dibleyi* Woodward : 38 ; fig. 3.
1907 *Pachyrhizodus dibleyi* Woodward : 128 ; pl. 26, figs 1–4.

Diagnosis (emended). Large species of *Pachyrhizodus* known only by fragments of upper jaw, dentary and endopterygoid ; teeth of upper jaw large, conical, not recurved, posterior teeth in maxilla showing marked anteroposterior compression, teeth irregularly spaced ; teeth in lower jaw conical.

Holotype. BM(NH) P.9115, imperfect premaxilla and maxilla, Lower Chalk (Zone of *Holaster subglobosus* – Upper Cenomanian, Kent, England.

Material. The holotype, also BM(NH) 49093, P.4806, P.10042, and SM B.94564–5.

Formation and Localities. Lower Chalk (Cenomanian), Kent, Surrey, and Sussex, England.

Other Species of *Pachyrhizodus*

Other species of *Pachyrhizodus* are known from North America and Australia. From North America, eight species of the genus have been described in works by Cope (1872, 1874, 1875), Loomis (1900) and Stewart (1898, 1899). Most of these species are based on isolated jaw fragments and it has become clear that there are, at most, two or three species involved. Applegate (1970) recognized three species, *Pachyrhizodus caninus* Cope, *P. kingi* Cope and *P. minimus* Stewart. Applegate (1970 : 411) noted that *P. kingi* may represent the juvenile form of *P. caninus*, but further remarked that the discontinuous size distribution and differences in the appearance of vertebral cross-sections may not support such a view. Dr David Bardack (personal communication) is also of the opinion that the American forms may be referred to two or, at most, three species.

The American species come from the Eagle Ford Shale, the Niobrara Chalk, the Austin Chalk, the Selma Chalk and the Mooreville Chalk. Together, these deposits range in age from Turonian to Campanian (Cobban & Reeside 1962, Stephenson *et al.* 1942). The American species are generally larger than most of the English species. The smallest, *P. minimus*, is approximately 900 mm long and is comparable to the estimated length of *P. subulidens*. The largest American species, *P. caninus*, is over 1800 mm long and is probably about the same size as *P. basalis*. Both these American species are very similar to the larger English species. In both, the skull roof is broad throughout particularly above the orbit, the roof is formed of thick bone and the depression in the frontals (interfrontal fossa of Applegate 1970) is well developed, the preoperculum is expanded posteroventrally and is broadly rounded, and the posterior infraorbitals are very wide and cover much of the operculum and suboperculum. The jaws are also very similar in the English and American species. The premaxillae of the American species are held horizontally (or nearly so) and this resembles the presumed condition in *P. basalis* and *P. dibleyi*. The ventral margin of the dentary in the American species is strongly inflected as in some English species.

At present, comparisons between English and American species can only be made at a superficial level, but I know of no facts that would refute considering these species as being congeneric. A particularly strong similarity in skull proportions and jaw morphology exists between the English *P. subulidens* and the American *P. minimus*. A detailed study of the latter may well reveal it to be conspecific with *P. subulidens*.

There are two points of difference between the English and American species that have yet to be explained. The large ' scale-bone ' which is reputed (Applegate 1970) to cover much of the operculum in the American species is not seen in the English species. This ' scale-bone ' could, of course, be an enlarged supratemporal or possibly the large dermosphenotic. Secondly, the English species do not show the paired rounded tooth-plates (Applegate 1970 : fig. 193c) that are either palatal or vomerine in origin. The vomer of the English species is relatively small and is certainly not a double structure while a tooth-bearing palatine has not yet been identified.

One species of *Pachyrhizodus* is known from Australia. *Pachyrhizodus marathonensis* (Etheridge) from marine deposits of the Albian of Queensland has been described by Bardack (1962) and Bartholomai (1969). BM(NH) P.55858 is a specimen of *P. marathonensis*. From the sketch (Fig. 33) of this specimen the typical *Pachyrhizodus* features may be seen : the frontal depression, large supraorbital, broad posterior infraorbitals, premaxilla with a broad dorsal process, small lateral expression of the angular, large preoperculum and the large outermost pectoral fin-ray. This specimen also shows a large basibranchial tooth plate and a spine-like anterior tip of the preoperculum, as in *Rhacolepis*. *Pachyrhizodus marathonensis* is the only species in which a fenestrated anterior ceratohyal is recorded. Bartholomai (1969) suggests that *P. marathonensis* is similar to *P. subulidens*, differing only in the narrower cranial roof and greater dorsal expression of the supraoccipital. Bartholomai (1969 : 255) mentions that the nasals of *P. marathonensis* are not preserved. In fact, nasals have not been described for any species of *Pachyrhizodus* and it is possible that nasals are absent from all species.

Mention must be made of *Thrissopater daguini* described by Arambourg (1954) from the Cenomanian of Jebel Tselfat, Morocco, although I have not seen either of the two specimens (Arambourg 1954 : 70) of *T. daguini* and can add nothing to his description. Arambourg referred this form to *Thrissopater* because of certain

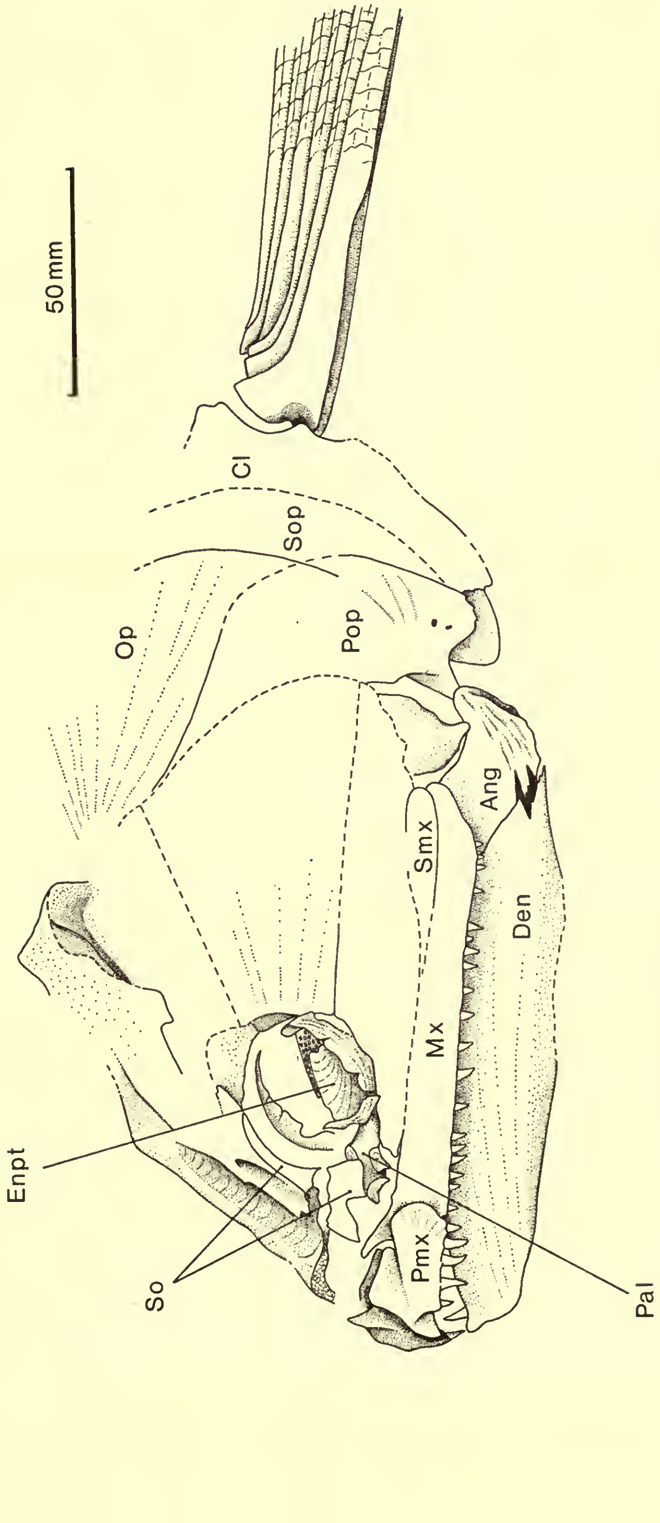
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FIG. 33. *Pachyrhizodus marathonensis* (Etheridge). Freehand sketch of left lateral view of BM(NH) P.55858.

similarities in the skull roof, particularly the small separated parietals and the depression in the frontals immediately anterior to the supraoccipital. He went on to compare the skull roof with certain stomiatoids using similar characteristics.

Similarities in the small, separated parietals and the presence of a frontal depression do not constitute strong evidence of relationship. There are several marked differences between other species of *Thrissopater* (=*Pachyrhizodus*) and *T. daguini*. The skull roof of the latter shows that the frontals are narrow above the orbit, the pterotic is very small and the main supraorbital sensory canal passes directly from the frontal to the pterotic (Arambourg 1954 : fig. 35). None of these features is seen in *Thrissopater*. The articulation of the quadrate with the mandibular ramus occurs below the middle of the orbit, unlike any species of *Thrissopater* (or *Pachyrhizodus*). The maxilla of *T. daguini* is apparently curved and distally expanded and the teeth on the maxilla and dentary are very small. *T. daguini* is a very small species, the length with the caudal fin being 110 mm (Arambourg 1954 : 75) in contrast to all other species. It is clear, from the inclusion of the maxilla in the gape and the form of the postcranial skeleton, that *T. daguini* is a lower teleostean fish but there is little (or perhaps no) evidence justifying its association with *Thrissopater*. *T. daguini* will not be considered further here.

Genus ***ELOPOPSIS*** Heckel 1856

The genus *Elopopsis* was erected by Heckel (1856), the type species being *E. fenzli* Heckel, from the Cenomanian of Comen, Jugoslavia. Four other species are recognized: *E. microdon* Heckel from the Cenomanian of Jugoslavia and the Lower Cenomanian of Morocco (Arambourg 1954), *E. heckeli* Reuss from the Cenomanian of Czechoslovakia, *E. ziegleri* (Marck) from the Campanian of Westphalia (this form may prove to be conspecific with *E. crassus*) and *E. crassus* Dixon from the *Rhynchonella cuvieri* Zone (Turonian) of Kent, south-east England. Only *Elopopsis crassus* and *E. microdon* are well enough known to deserve comment, and the only species studied in this work is *E. crassus*. The following descriptive remarks are based on seven specimens: BM(NH) P.10217, P.10218, P.10320, P.10337, P.10619, P.11201 and P.11907. All come from the Turonian of south-east England. For diagnoses of this species and the genus see Woodward (1908: 132–133).

Descriptive remarks. The skull roof is composed of thin bone, unlike *Pachyrhizodus*, to which it is otherwise similar. The roof is broad and in the otic region is convex in the transverse plane. The frontals (Fig. 34, Fr) are large and are marked by prominent growth ridges. Anteriorly the frontals may have overlapped one another. A frontal depression is present, as in *Pachyrhizodus*. The parietals are not seen clearly in any specimen but they appear to have been small with irregular margins and to have been separated by the supraoccipital. The dermethmoid (Fig. 34, De) is very broad and the posterior margin overlaps the frontals in a zigzag fashion. From the underside of the dermethmoid projects a pair of ventrolateral processes, as in *Rhacolepis*. A mesethmoid is present but the limits of this ossification are unknown.

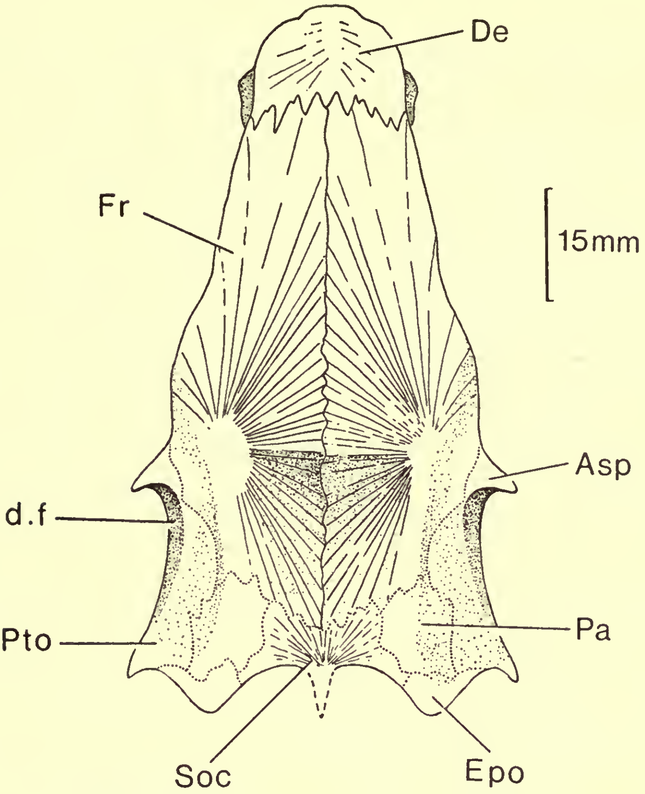

FIG. 34. *Elopopsis crassus* (Dixon). Braincase in dorsal view. Based on BM(NH) P.10218.

The hyomandibular slopes slightly backwards (as in *E. microdon*) in contrast to the vertical hyomandibular of *Pachyrhizodus*. There is a prominent ridge upon the hyomandibular.

There are five infraorbitals known in *E. crassus*. The first is large and is distinctive in that the contained infraorbital sensory canal sends off several branches which radiate from a common origin. The second, which may represent fused second and third infraorbitals, is relatively smaller than the corresponding element in *Pachyrhizodus*. The posterior infraorbitals are rather narrow and do not reach the preoperculum. Narrow posterior infraorbitals may be a specific character of *E. crassus*. *Elopopsis microdon* shows broad posterior infraorbitals (Fig. 35B). The orbit is relatively large in both *E. crassus* and *E. microdon*.

The upper and lower jaws are relatively shorter than in most species of *Pachyrhizodus*. The upper jaw ends beneath the posterior border of the orbit as in *Pachyrhizodus megalops*; the lower jaw ends slightly behind this level. The oral margin of the maxilla is convex and the head of the maxilla is turned slightly inwards and bears a small dorsal ridge which probably articulated with the palatine. There is a single supramaxilla which is relatively broader than that seen

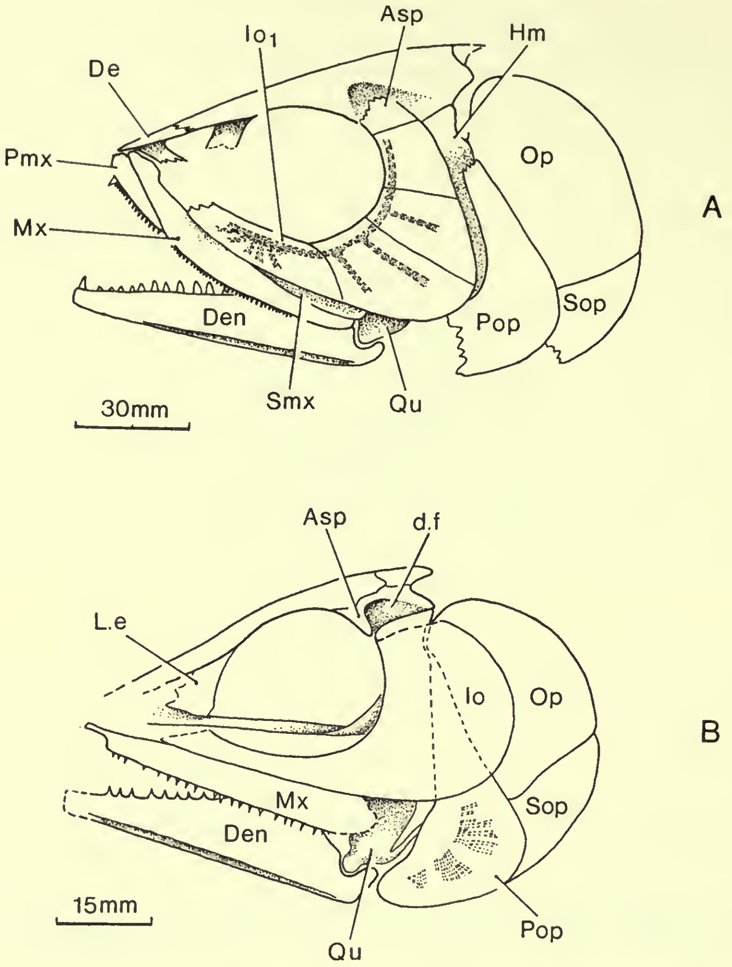

FIG. 35. *Elopopsis*. Outline restorations of the cranium of: A, *Elopopsis crassus* (Dixon); B, *E. microdon* Heckel.

Pachyrhizodus. The curved oral margin of the maxilla is not a generic character of *Elopopsis* since *E. microdon* shows a straight maxillary margin as in *Pachyrhizodus*. The premaxilla is triangular and, as Woodward (1908) notes, is expanded horizontally, as in the American species of *Pachyrhizodus*. The mandibular ramus is shallow with a weakly defined coronoid process and is without an inflected ventral margin. Posteriorly, there is a prominent postarticular process.

The dentition has been well described by Woodward (1908). Similarities with *Pachyrhizodus* include prominent inner premaxillary teeth with an outer single row of smaller teeth. The maxilla bears a single row of teeth; the dentary also bears a single row of teeth throughout most of its length but unlike *Pachyrhizodus* there is an enlarged symphysial tooth. The inner premaxillary teeth and the teeth on the dentary are laterally compressed, a feature never seen in *Pachyrhizodus*. Behind the symphysial tooth the teeth on the dentary gradually increase in size posteriorly. In *E. microdon* the dentary teeth are of uniform size, although as in *E. crassus* they are laterally compressed.

The anterior ceratohyal is fenestrated, as in *Rhacolepis* and *Notelops*. There are numerous branchiostegal rays, at least 17 of which can be identified in BM(NH) P.10218. The opercular bones are very thin, as in *Pachyrhizodus*, and the preopercular sensory canal is profusely branched.

The scales are large and deeply overlapping, as in *Notelops* and *Rhacolepis*. The posterior field is marked by small pits and many evenly-spaced circuli are present (Woodward 1908 : pl. 28, fig. 4). Above the origin of the pectoral fin the scales are contoured into a groove which receives the outermost fin-ray and the posterior elongation of the lower postcleithrum. In all, the squamation in this area is very similar to that in *Pachyrhizodus salmoneus*.

There are enough facts known to suggest that *Elopopsis crassus* is similar to *Pachyrhizodus*. More detailed information about *E. crassus* is required, however, before an assessment of its relationships with *Pachyrhizodus*, *Notelops* and *Rhacolepis* can be made.

Arambourg (1954) provided some information on the postcranial skeleton of *Elopopsis microdon*, a small species about 300 mm long. The structure of the caudal skeleton and fin is of interest (Arambourg 1954 : fig. 33 ; pl. 7, fig. 3). The base of the first uroneural is somewhat expanded and overlaps much of the first preural centrum. It resembles *Rhacolepis* in the double nature of the third preural centrum in the specimen figured by Arambourg (fig. 33) and in the ornamentation on this and the preceding centrum.

The neural and haemal arches appear fused with the supporting centra. As in *Rhacolepis* the fin-rays cover much of the hypurals and there are both dorsal and ventral caudal scutes. Further resemblances to *Rhacolepis* are the short paired fins, the origin of the pelvics behind the level of the dorsal fin and the very small scales (as in *Rhacolepis buccalis*). *Elopopsis microdon* apparently shows a series of epipleural intermuscular bones, not seen in any of the fishes grouped here as pachyrhizodontoids.

IV. DISCUSSION

(a). Relationships of *Notelops*, *Rhacolepis* and *Pachyrhizodus*

Features of the three genera which are pertinent to discussions of relationship may be listed as follows:

1. Supraoccipital small, supraoccipital crest weakly developed.
2. Nasals small, tubular (unknown in *Pachyrhizodus*).
3. Supratemporal large, scale-like.
4. Dilatator fossa large.
5. Post-temporal fossa roofed.
6. Otic region of the neurocranium fully ossified.
7. Orbitosphenoid and basisphenoid present.

8. Pars jugularis long ; separate lateral openings for the hyomandibular ramus of VII, jugular vein and orbital artery.
9. Hyomandibular with single articulatory head.
10. Hyomandibular ramus of VII leaving the hyomandibular beneath the opercular process and running in a groove on the posterior margin.
11. Endopterygoid with many small teeth.
12. Palatine without a maxillary process.
13. Hyoid bar consisting of anterior and posterior ceratohyals separated by a narrow band of cartilage. Two hypohyals present.
14. Chondral elements of gill arches ossified, remaining separate from the dermal tooth-plates (unknown in *Pachyrhizodus*).
15. Branchiostegals numerous.
16. Opercular apparatus complete, with large suboperculum and interoperculum.
17. Ribs absent from first two vertebrae.
18. Anterior neural arches and parapophyses autogenous.
19. Epineurals fused with neural arches in abdominal region (unknown in *Pachyrhizodus*).
20. Epipleurals and epicentrals absent (unknown in *Pachyrhizodus*).
21. Anterior neural arches formed in separate lateral halves.
22. Mesocoracoid arch present, united ventrally with both the scapula and coracoid.
23. Two postcleithra.
24. Pectoral fin low on flank, with about 16 rays.
25. Pelvic fins abdominal.
26. Inner pelvic radial spine-like, remaining free from the girdle (unknown in *Pachyrhizodus*).
27. Anal fin small and remote.
28. Caudal fin forked, with 19 principal rays (count not known in *Pachyrhizodus*).
29. Scales cycloid, with bone-cell spaces.
30. Second preural centrum bearing a half-length neural spine.
31. Snout consisting of a large dermethmoid and (except in large species of *Pachyrhizodus*) cartilaginous ethmoid.
32. Frontals large, constituting most of the skull roof.
33. Parietals small.
34. Parietal branch of supraorbital sensory canal absent.
35. Occipital condyle formed entirely by basioccipital.
36. Saccular region of neurocranium not inflated.
37. Parasphenoid without teeth.
38. Basipterygoid process absent.
39. Hyomandibular with well-developed lateral process (ridge) adjacent to the opercular process.
40. Upper jaw in which the premaxilla bears a dorsal process (? articular process) ; maxilla fitting tightly against the premaxilla ; single supramaxilla.
41. Circumorbital series in which the supraorbital is very large, a separate antorbital is absent, the second and third infraorbitals are fused together, and the dermosphenotic is very large and contains a posterior branch of the sensory canal.

42. Pectoral splint absent.
43. Pelvic bones meeting posteriorly in a cartilaginous symphysis (unknown in *Pachyrhizodus*).
44. Posterior neural arches, parapophyses and haemal arches fused with centra.
45. Caudal skeleton in which the parhypural is fused with the first preural centrum, the first ural centrum with a compound element representing the first and second hypurals, and there are varying degrees of fusion between upper hypurals.

Features listed against numbers 1–30 are primitive teleostean characters, showing only that the three genera are at a primitive teleostean grade. Features 31–45 are all advanced in some degree over the basic teleostean plan. Of these features 41 and 45 are particularly significant, serving to show that *Notelops*, *Rhacolepis* and *Pachyrhizodus* form a monophyletic group.

The pattern of circumorbitals in pachyrhizondontoids shows several features that are advanced in relation to the basic teleostean condition as proposed by Nelson (1969).* In pachyrhizodontoids there is no separate antorbital, the second and third infraorbitals are fused together, there is a posterior branch of the sensory canal within the dermosphenotic and the latter is in sutural contact with the large supraorbital – an exception to the last feature is seen in *Pachyrhizodus megalops* where the supraorbital and dermosphenotic just touch one another. Additionally, in *Notelops* the fourth and fifth infraorbitals are fused together as in *Gaudryella* Patterson (1970b : 219).

The fate of the antorbital in pachyrhizodontoids (and, indeed, most other 'lower teleosteans') is not known. It could have fused with the first infraorbital as in some osteoglossoid fishes (Nelson 1969 : fig. 12) or with the supraorbital, it could have been lost altogether, or it could have fused with the lateral ethmoid (as has possibly happened in *Hiodon*, according to Greenwood & Patterson 1967 : 215). The last possibility is rejected for the pachyrhizodontoids since there is no dermal component in the lateral ethmoid. Comparisons with the osteoglossoids suggest that the antorbital is not fused with the first infraorbital in the same manner. In *Arapaima* and *Heterotis* (Nelson 1969 : fig. 12) the shape of the compound anterior element and the path of the contained sensory canal strongly suggest a fused antorbital and first infraorbital. In pachyrhizodontoids the infraorbital sensory canal runs to the tip of the first infraorbital without turning dorsally. It should be noted at this point that there is no similarity between the circumorbitals of osteoglossomorphs and pachyrhizodontoids. There is no supraorbital in osteoglossomorphs and where there is fusion of the infraorbitals it occurs between the third and fourth members of the series (Nelson 1969). Elsewhere among 'lower teleosts', loss of a separate antorbital is restricted† to euteleosts. Thus, the absence of a separate antorbital is noted in *Esox* and *Umbra* (Gosline 1961 : 28), *Galaxias* (Gosline 1961 : 28 ; McDowall 1969 : fig. 3B), *Retropinna osmeroides* and *Prototroctes maraena* (McDowall 1969 : fig. 3A, E), *Gonorhynchus* (Gosline 1961 : 28), *Hoplias malabaricus* (Weitzman 1962 : 29), *Erythrinus unitaeniatus* (Gregory 1933 : fig. 67) and *Opsariichthys hainanensis* (Nelson 1969 : fig. 5B). It generally disappears in cyprinids, according to Gosline (1961 : 30). In these euteleosts, as in the pachyrhizodontoids, there is no direct evidence that the antorbital has fused with the first infraorbital. It is probable that a separate antorbital has been lost many times within 'lower euteleosts' and this may be related to the absence of a supraorbital nasal diverticulum (see Gosline 1961 for details of this structure).

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* Nelson (1969) was concerned with the canal-bearing bones of the infraorbital series. It may safely be assumed that at least one supraorbital is also present in the primitive teleostean condition. Furthermore, it is suggested that the primitive supraorbital is a small splint-like element. This, at least, is its form in the vast majority of 'lower teleostean' fishes and in pholidophorids (Nybelin 1966).

† It is possible that the antorbital of some eels has been fused with ethmoid bones since the snout of many eels is a highly consolidated structure. However, there is a separate antorbital in *Simenchelys parasiticus* (McDowell 1973 : fig. 1F), *Synaphobranchus* (Robins 1971 : fig. 1) and in *Atractodenchelys phrix* and *Dysommia* (Robins & Robins 1970 : fig. 3).

Fusion between members of the infraorbital series lying below and behind the orbit in 'lower teleosts' has been noted by Nelson (1969). In all cases it involves fusion between the third and fourth infraorbitals of the teleostean morphotype. Pachyrhizodontoids are therefore unusual in showing fusion between the second and third infraorbitals.

The dermosphenotic of pachyrhizodontoids is very large. It covers most of the dilatator fossa and has, in addition to the characteristic Y-shaped division of the infraorbital canal, an additional posteriorly-directed branch (or branches as in the case of *Pachyrhizodus megalops*). The only other 'lower teleosts' in which a similar branch is recorded are some salmonids figured by Nelson (1969 : fig. 7) : *Salmo gairdneri*, *S. trutta*, *Brachymystax lenok* and *Oncorhynchus nerka*. Such a branch is also present in *Oncorhynchus keta*. Elsewhere among 'lower teleosts' there is either no posterior branch-opening in the dermosphenotic or the opening occurs at the junction of the fifth infraorbital with the dermosphenotic.

A large supraorbital which is sutured with the dermosphenotic as in the pachyrhizodontoids is relatively rare in lower teleosts, although it is seen in some characins and catfishes. No phylogenetic inferences may be drawn from this similarity.

In sum, the circumorbital series of the pachyrhizodontoids is distinctive in showing fusion between the second and third infraorbitals and the large size of the dermosphenotic and posterior infraorbitals. Where similarities exist with other 'lower teleosts' these are shared with euteleosts. However, there is no one particular group of euteleosts that is directly comparable with pachyrhizodontoids in this respect.

The caudal skeleton is known (at least, in part) in *Notelops*, *Rhacolepis* and the American species of *Pachyrhizodus* (Fig. 36 ; Hay 1903 : pl. 3 ; Nelson 1973a : fig. 8A). In these forms the caudal skeleton shares important similarities in the pattern of fusion which appears to be unique among 'lower teleostean' fishes.

The parhypural, which bears a small hypurapophysis in *Rhacolepis* and *Pachyrhizodus*, is fused with the first preural centrum. The first and second hypurals are fused together and to the first ural centrum. There may also be some degree of fusion between the upper hypurals. Fusion between members of the hypural series is probably of little significance since it is subject to individual variation and may even be an ontogenetic phenomenon. It is a common occurrence in euteleosts. Fusion of lower hypurals and the parhypural with supporting centra is common throughout euteleosts but I know of no instance in which this has taken place without prior fusion between the first ural centrum and the first preural centrum.

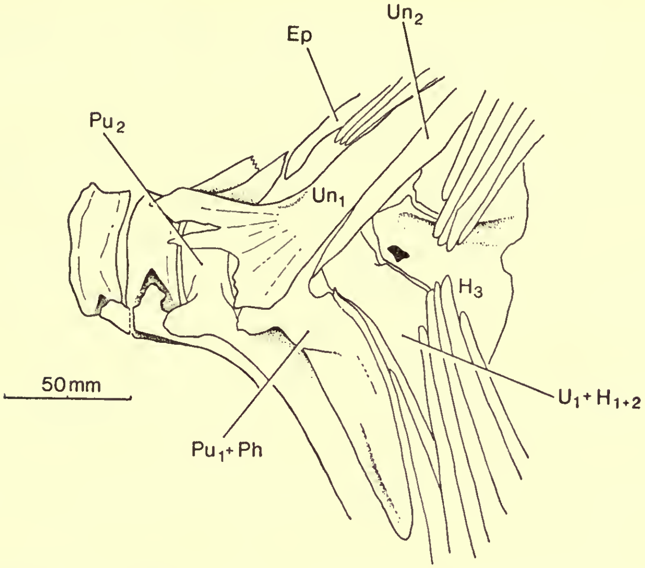

FIG. 36. *Pachyrhizodus caninus* Cope. Freehand sketch of the caudal skeleton as represented in SMU 62406.

Outside the euteleostean fishes fusion between the parhypural and supporting centrum is rare but is recorded in the osteoglossomorphs *Hiodon alosoides* (Gosline 1960 : fig. 4 ; Patterson 1968 : fig. 11) and *Notopterus notopterus* (Nelson 1969 : fig. 20D), and in the clupeomorphs *Denticeps* (Greenwood 1968 : fig. 29), *Ornategulum* and *Diplomystus analis* (Forey 1973a : figs 7, 9A). Fusion of the second hypural with the supporting centrum is characteristic of clupeomorphs (and ostariophysans), but in these fishes this fusion is associated with the freeing of the first hypural, fusion of the anterior uroneural with the first preural centrum and a rather long second ural centrum. None of these associated features is seen in the pachyrhizodontoid caudal skeleton.

There are usually two uroneurals in pachyrhizodontoids, perhaps three in *Notelops*, the first of which is large and expanded (*Notelops*) or forked proximally (*Rhacolepis* and *Pachyrhizodus*). The proximal forking is particularly well developed in *Pachyrhizodus* (Fig. 36 ; Hay 1903 : pl. 3) and this may be an adaptive feature serving to strengthen the skeleton. The caudal fin of *Pachyrhizodus* is very deep and exhibits a high degree of hypurostegy. The base of the anterior uroneural bears a narrow anterior expansion but this is not as well developed as that expansion associated with the first uroneural ('stegural') of salmonoids or osmeroids. The second uroneural is primitively long, reaching to cover the lateral face of the first ural centrum.

In *Rhacolepis* the first preural neural arch is fused with its supporting centrum ; the condition in *Notelops* and *Pachyrhizodus* remains unknown. Similar fusion is seen in clupeomorphs, ostariophysans and some protacanthopterygians (Patterson 1970b).

In sum, the pachyrhizodontoid caudal skeleton is unique among 'lower teleostean' fishes. It is basically primitive, with the few specialized features being seen most commonly in euteleosts. However, fusion between the first ural and first preural centra, so characteristic of euteleosts, has not taken place in pachyrhizodontoids. In those euteleosts in which these centra are not fused (alepocephaloids, esocoids and salmonids) the parhypural and hypurals are also autogenous (more primitive than pachyrhizodontoids) or there is a well-developed 'stegural' present (esocoids and salmonoids, which are therefore more advanced than pachyrhizodontoids in this respect). Features of these two character complexes (circumorbital series and the caudal skeleton) show that *Notelops*, *Rhacolepis* and *Pachyrhizodus* are their own closest relatives.

Notelops, *Rhacolepis* and *Pachyrhizodus* have traditionally been associated with elopoids (Elopiformes), but apart from many shared primitive characters (nos 1–19 and 21–30 from the list, pp. 183–5) they seem to have little in common with the latter. Among the advanced characters listed for pachyrhizodontoids, nos 31 and 37–39 are known in elopoids. These can hardly be regarded as evidence of close relationship since they are also known, for instance, in protacanthopterygians. More importantly, pachyrhizodontoids are not known to have the elopoid characteristics of rostral ossicles or prenasal ossicles (Gosline 1961, Forey 1973b) or fusion between the angular and retroarticular (Nelson 1973a, b). In many characters (e.g. nos 32–36 and 40–45) pachyrhizontoids are more advanced than elopoids.

Pachyrhizodontoids do not share any uniquely specialized features with osteoglossomorphs (or ichthyodectids) and the typical derived characteristics of osteoglossomorphs (Greenwood 1966, Greenwood *et al.* 1966, Nelson 1969, 1972) are absent from *Notelops*, *Rhacolepis* and *Pachyrhizodus*.

Similarly, pachyrhizodontoids do not show any clupeomorph characteristics (for these see Greenwood 1968, Greenwood *et al.* 1966, Patterson 1970a) or the occipito-cervical vertebral and rib specializations of the Ostariophysii (*sensu* Rosen & Greenwood 1970) and cannot be considered closely related to either of these superorders.

The remaining 'lower teleostean' group is the Protacanthopterygii, containing only the Salmoniformes. Unfortunately, it is at present impossible to define the Protacanthopterygii satisfactorily, or to suggest the interrelationships between the constituent members (Patterson 1970b). For this reason it is difficult to justify the inclusion of the pachyrhizontoids within the Salmoniformes (or, for that matter, to justify their exclusion). Within the salmoniforms the Salmonoidei, and in particular the Salmonidae, appear to have retained the greatest number of primitive teleostean characters, but this does not mean to say that they are the 'basal stock', as has been assumed, e.g. by McDowall (1969 : 817). A comparison between pachyrhizodontoids and protacanthopterygians shows that there are similarities in certain 'advanced' features, i.e. those thought not to be present in the basic teleostean plan. In some features a resemblance is noted to the large-mouthed salmonids (the salmonines).

Certain features (nos 31–38 listed above, p. 184) are commonly found in protacanthopterygians, and in particular there is a general resemblance between the skull roof of *Rhacolepis*, *Pachyrhizodus* and the salmonines. These resemblances include the large dermethmoid which is rather blunt anteriorly, the very large frontals and the small, separated parietals. Of the characters nos 31–38, only 35 is not known to occur in all salmonids since, according to Cavender & Miller (1972 : 30), salmonines show a tripartite occipital condyle, which is presumably more primitive than a condyle formed by the basioccipital alone. The resemblances in the skull roof must be due to convergence or, at best, parallelism, since *Notelops* is more primitive in showing medially united parietals, a subtemporal fossa and a prootic–intercalar bridge.

In the hyopalatine series Patterson (1970b) notes the absence of ectopterygoid teeth in all salmoniforms, although there is some doubt as to whether they are absent in *Retropinna* (Weitzman 1967, McDowall 1969) ; this is an undoubtedly derived character. Among the pachyrhizodontoids *Rhacolepis* shows ectopterygoid teeth. In *Notelops* the toothed palatine has grown back to replace functionally the ectopterygoid as in many salmoniforms.

The upper jaw of the pachyrhizodontoids shows some similarity with that of salmonines (Fig. 37, and see illustrations in Norden 1961 and Vladykov 1962). In both the premaxilla is small and bears a dorsal process (the articular process in salmonids). The maxilla has a simple head, a poorly developed palatine process (absent in some) and a long 'blade' with a small, splint-like supramaxilla. The dentition is also similar, with a series of robust teeth set in pleurodont fashion. The premaxilla of salmonines may bear inner teeth.

The anatomy of the lower jaw of pachyrhizodontoids is somewhat variable. Since the anatomy of the lower jaw of 'lower teleostean' fishes has been the subject of recent discussion by Nelson (1973a, b) it is appropriate to discuss the lower jaws of *Notelops*, *Rhacolepis* and *Pachyrhizodus* in the broad terms of reference he provided. Nelson discusses three aspects of the lower jaw which he found to be subject to some variation – the composition of the articulatory facet, the pattern of fusion between the bones at the posterior end of the jaw and the position of the sensory canal opening.

With respect to the articulation facet, Nelson (1973a) postulated that the primitive teleostean condition shows the development of the facet on the articular and the retroarticular, e.g. as in *Heterotis*. In the pachyrhizodontoids the retroarticular takes no part in the facet and in this they resemble clupeomorphs, euteleosts and ichthyodectids. In *Notelops* the articulation facet is formed from contributions by the separate articular and angular. In *Rhacolepis* and the American species of *Pachyrhizodus* (Nelson 1973a : fig. 2c), in which the angular and articular are fused together, the articulation facet is formed by both articular and angular contributions.

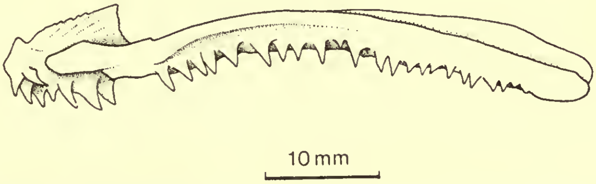

FIG. 37. *Salmo clarki* Richardson. Upper jaw of right side, in medial view.

Thus pachyrhizodontoids are more advanced than the proposed basic teleostean condition in showing an angular (i.e. dermal) contribution to the facet. In this, they resemble clupeomorphs, euteleosts and ichthyodectids and possibly also elopomorphs and ananogmiids (Nelson 1973a).

In *Notelops* the angular, articular and retroarticular are separate ossifications and this is certainly primitive with respect to *Rhacolepis* in which there is a compound angulo-articular and separate retroarticular. The American species of *Pachyrhizodus* are apparently similar to *Rhacolepis* (Nelson 1973a). Conditions in the English species of *Pachyrhizodus* could not be determined because of the lack of suitable material. The unfused condition of the bones in *Notelops* resembles that in certain osteoglossoids and ichthyodectids (Nelson 1973a, b) but since this is presumed to be the primitive teleostean condition no phyletic significance may be inferred from the resemblance. The fusion pattern in the lower jaw of *Rhacolepis* and the American species of *Pachyrhizodus* is similar to that seen in clupeomorphs and euteleosts.

The position of the sensory canal opening in pachyrhizodontoids is not clear. Nelson (1973a) was unable to determine its position in American species of *Pachyrhizodus*. In both *Notelops* and *Rhacolepis* there is a series of pores (only one in the young specimen of *Notelops* shown in Fig. 4) opening onto the lateral surface of the angular (or angulo-articular). The most posterior of these pores lies near the tip of the postarticular process. However, there is also a pore, presumably for the sensory canal, on the medial face of the angular (angulo-articular), located just behind the articulatory facet and in a comparable position to the medial opening in *Elops* and *Megalops* (Nelson 1973a). In *Rhacolepis*, this pore leads to a canal which joins the main mandibular canal at the dentary/angulo-articular overlap. It was not possible to determine where the pore led in *Notelops*. Nelson (1973a) suggested that a medial opening of the sensory canal is a derived teleostean character found in elopiforms, ichthyodectids and ananogmiids. However, Patterson & Rosen (in press) show, in convincing fashion, that the medial opening for the sensory canal is a primitive feature for teleosts and thereby invalidate its use as evidence of relationship.

One further feature of the lower jaw noted by Nelson (1973a, b) is a 'reverse overlap' of the angular and dentary near the coronoid process in elopiforms, characoids and clupeomorphs. Both *Notelops* and *Rhacolepis* show such a 'reverse overlap', which is also seen in the salmonid *Stenodus leucichthys* figured by Cavender (1970 : fig. 7E). The significance of this overlap is not clear.

To summarize the lower jaw evidence in the terms of reference provided by Nelson (1973a, b) : *Notelops* is more primitive than most 'lower teleosts' in showing unfused articular, angular and retroarticular bones ; *Rhacolepis* and the American species of *Pachyrhizodus* resemble clupeomorphs and euteleosts in the fusion pattern. It follows that if *Notelops* is more closely related to *Rhacolepis* and *Pachyrhizodus* than to any other teleost, fusion between the angular and articular must have occurred independently in this lineage as it has apparently in the osteoglossomorph lineage (Nelson 1973b).

A general resemblance may be noted between the lower jaw of *Rhacolepis*, *Pachyrhizodus* and the salmonines (Fig. 38). Resemblances are seen in the dentition,

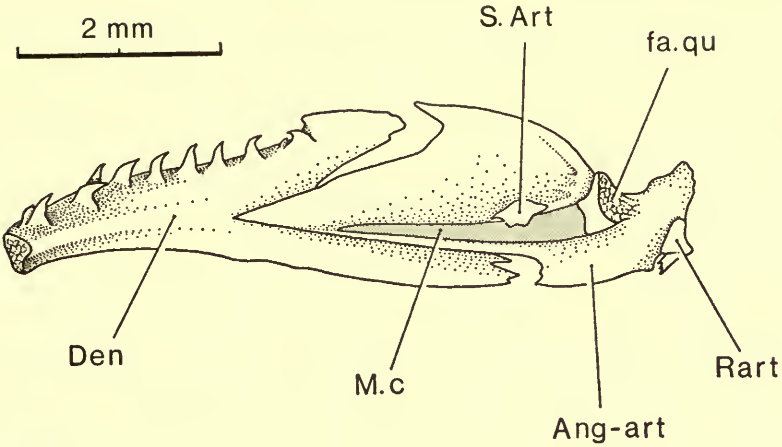

FIG. 38. *Salmo trutta* Linnaeus. Right mandibular ramus of a young individual, in medial view.

the shape and position of the retroarticular and the shape of the articulatory facet and postarticular process. However, despite these resemblances in shape there is no unique shared derived character that would suggest close relationship.

The pectoral girdle and fin of pachyrhizodontoids are basically primitive and I know of no details here that could be useful in suggesting relationship. The pelvic girdle consists of two pelvic bones that are united posteriorly in a cartilaginous symphysis such as is seen in many protacanthopterygians, including all salmonids. The vertebral column shows fusion between the centra and the posterior parapophyses, haemal arches and the neural arches in the caudal region. Again this is also seen in salmonids where there is also the incipient development of zygapophyses as seen in *Rhacolepis*. Primitively, the pachyrhizodontoid and salmonid vertebral columns lack epicentral or epipleural intermusculars : I have been unable to confirm the presence of epipleurals in *Thymallus arcticus* recorded by Norden (1961).

Despite the osteological similarities between pachyrhizontoids and the salmonines there is no good evidence (i.e. a unique shared derived character) that a close phylogenetic relationship exists. Comparisons between pachyrhizodontoids and the more derived salmoniforms (osmeroids, argentinoids, galaxioids, stomiatoids, alepocephaloids, giganturoids and esocoids) lead to the same conclusion. In fact, it seems that among the protacanthopterygians the salmonoids are 'closest' to the pachyrhizodontoids, but this is probably only because both are of primitive teleostean grade.

Patterson (1970b) has shown that on the basis of caudal anatomy, the protacanthopterygians may be divisible into two groups. *Rhacolepis* agrees with the alepocephaloid–argentinoid grouping in showing fusion between the first preural neural arch and the supporting centrum, and all pachyrhizodontoids agree with this grouping in lacking a 'stegural' (irrespective of how that structure may be formed).

However, the haemal elements are never fused with centra in the alepocephaloid-argentinoid group and the full-length second preural neural spine of these fishes is more specialized than the half-length spine of pachyrhizodontoids.

There is probably no advantage to be gained in attempting to compare morphotypes (*sensu* Zangerl 1948) of the Protacanthopterygii and the Pachyrhizodontoidei. It would be impossible to establish a protacanthopterygian morphotype on present evidence since, with the possible exception of the toothless ectopterygoid, there are no unifying characters of this group (i.e. monophyly has not been demonstrated) and the interrelationships of the salmoniform suborders are not sufficiently well understood. McDowall (1969) did attempt to deduce a salmonoid morphotype, and since that author believed salmonoids to be the basal protacanthopterygian stock it would also be the salmoniform morphotype, but it proves to be of little use since nearly all the osteological features mentioned are primitive teleostean features. The exception in McDowall's (1969) description of the morphotype is the condition of the snout ossification which was hypothesized using the snout analysis made by Weitzman (1967). Patterson (1970b) justifiably criticizes this analysis, reversing the polarity of the morphocline and resulting in the primitive salmonoid having at least a perichondrally ossified mesethmoid, lateral ethmoids and a separate dermethmoid.

At present, the most that can be said about the relationships of the pachyrhizodontoids is that they are a group of primitive teleostean fishes showing certain derived features seen in euteleosts. However, the Euteleostei cannot yet be critically defined (Nelson 1973a) and therefore there is no logical basis for including the pachyrhizodontoids with an indefinable group. Within the Euteleostei they do not show any ostariophysan features, but do show some resemblance to salmonids. None of these resemblances can be regarded as evidence of relationship. The pachyrhizodontoids cannot be assigned to any existing suborder and must therefore be recognized as possessing, at least, subordinal status and be recognized as Teleostei *incertae sedis*. It is to be noted that Nelson (1973b) recognized *Pachyrhizodus* as Teleostei *incertae sedis*.

(b). Intrarelationships and evolution within the Pachyrhizodontoidei

From Table 1 (which excludes character states of doubtful phylogenetic significance, e.g. the fenestrations in the dilatator fossa of *Notelops* and the development of the prootic cup in *Pachyrhizodus*) it may be seen that *Rhacolepis* and *Pachyrhizodus* are similar to one another in sharing the derived states of characters 1–2, 4–9 and 12. On this basis *Rhacolepis* and *Pachyrhizodus* are 'sister-groups', but I find it impossible to decide which of the two genera is the apomorph. *Notelops* stands as the plesiomorphic 'sister-group' of *Rhacolepis* and *Pachyrhizodus*. *Notelops* appears to be derived, with respect to the pachyrhizodontids, in two features, the fusion of the fourth and fifth infraorbitals and in character 11 (Table 1). That the pachyrhizodontids have secondarily acquired a short palatine and a toothed ectopterygoid is unlikely, but the possibility cannot be ruled out. In *Rhacolepis* the ectopterygoid bears a single row of pointed teeth which is certainly

TABLE I

Similarities and differences in certain cranial characters between *Notelops*, *Rhacolepis* and *Pachyrhizodus*

	Notelops	*Rhacolepis*	*Pachyrhizodus*
1. Parietals	medially united	separated	separated
2. Frontal	lateral margin 'entire'	lateral margin 'excavated' above autosphenotic	lateral margin 'excavated' above autosphenotic
3. Pterotic spine	poorly developed	well developed	poorly developed
4. Subtemporal fossa	present	absent	absent
5. Prootic-intercalar bridge	present	absent	absent
6. Trigeminal foramen	opening into pars jugularis	opening directly to orbit	opening directly to orbit
7. Myodome	closed posteriorly	open posteriorly	open posteriorly (at least in *P. megalops*)
8. Parasphenoid	shallow beneath otic region	deep beneath otic region	deep beneath otic region
9. Fusion pattern in mandibular ramus	separate angular, articular and retroarticular	angulo-articular and retroarticular	angulo-articular and retroarticular (American species)
10. Dentition in dentary	several rows	single row	single row
11. Palate	palatine long, functionally replacing the edentulous ectopterygoid	palatine short, ectopterygoid with teeth	palatine short, ectopterygoid with teeth
12. Gular plate	present	absent	absent

unlike the presumed primitive teleostean condition in which there is a band of small villiform teeth. The absence of a pterotic spine (character 3, Table 1) in *Notelops* and *Pachyrhizodus* is surely a primitive feature. Based on the available facts there is no evidence to refute the suggested phylogeny outlined above. A classification to reflect this hypothesis places *Rhacolepis* and *Pachyrhizodus* in the family Pachyrhizodontidae and *Notelops* in the co-ordinate family Notelopidae.

Accepting the above phylogenetic interpretation (it is the most parsimonious and assumes no parallelism or convergence) certain 'phylogenetic trends' (morphoclines), can be recognized. The skull roof becomes broader, particularly above the orbit, and the frontals increase in relative size. In the otic region of the braincase the roof becomes broader and more convex, the roof of the dilatator fossa becomes very narrow, or absent altogether, above the autosphenotic, the autosphenotic spine increases in relative size and the subtemporal fossa disappears. These changes are probably interrelated and are concerned with the lateral movements of the hyomandibular and opercular apparatus. Erosion of the roof of the dilatator fossa and, to a lesser degree, the increase in the size of the autosphenotic spine allow the dilatator operculi muscle to spread dorsally. The increased size of the autosphenotic spine may reflect an increase in the bulk of levator arcus palatini musculature and, because it is located directly above the metapterygoid, is presumably in a position that would enhance the mechanical advantage of the levator muscle. The loss of the subtemporal fossa is probably related to the broadening and increased convexity of the otic region. In *Elops*, which like *Notelops* has a rather flat skull roof and a subtemporal fossa, the position of the hyomandibular facet relative to the lateral neurocranial wall is such that, were a subtemporal fossa absent, the distance between the medial surface of the hyomandibular and the neurocranial wall would be very short. In *Elops* the adductor hyomandibulae originates from the anterior half of the subtemporal fossa. The development of a subtemporal fossa effectively increases this distance and allows for a greater length (and hence a greater efficiency) of adductor hyomandibulae muscle to be accommodated (Fig. 39). In *Rhacolepis* and *Pachyrhizodus* the hyomandibular facet is drawn away from the lateral neurocranial wall at the level of the adductor origin by a broadening and increased convexity of the skull roof, so space for a suitable length of adductor hyomandibulae muscle is achieved without the need to develop a subtemporal fossa (Fig. 39). Since both structural designs allow for a reasonable length of adductor muscle it is difficult to judge which is the more efficient. However, the subtemporal fossa encroaches upon the lumen of the post-temporal fossa which receives some epaxial musculature. It also restricts the brain and perilymphatic cavities. The *Pachyrhizodus* plan does not impose these restrictions upon these cavities.

In the jaws, the dorsal process of the premaxilla becomes larger, the dentary becomes more robust and an inflected margin develops. The dentition becomes more powerful.

The posterior infraorbitals and the preoperculum become large, covering much of the operculum and suboperculum. The significance of these changes is not known. There is a trend towards an increase in the degree of branching of the preopercular sensory canal.

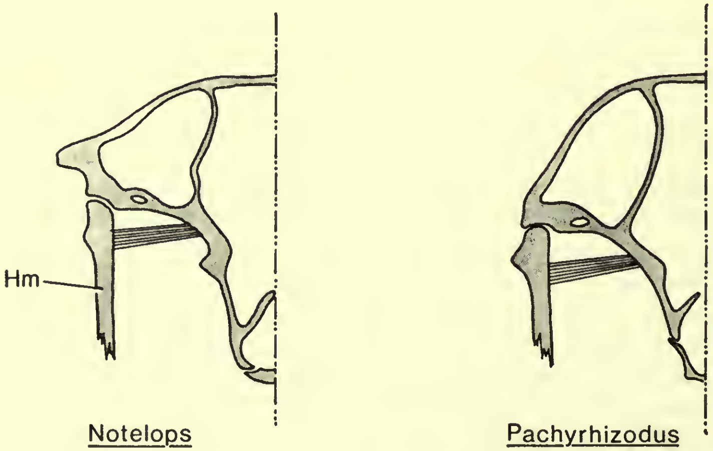

FIG. 39. Transverse sections through the otic region of the braincase and the hyomandibular of *Notelops* and *Pachyrhizodus*, to show the importance of the subtemporal fossa with respect to the length of the adductor hyomandibulae (converging lines).

The pachyrhizodontoids were probably powerful swimmers and were certainly carnivorous. Specimens of *Rhacolepis* contain leptolepid fragments within the abdominal cavity. The caudal fin of the American species of *Pachyrhizodus* is very deep and probably had a high aspect ratio suggesting that these species at least were capable of fast, sustained swimming. The well-developed teeth, distributed mainly on the dermal jaws, and the absence of parasphenoid teeth denote that the primary bite is between the lower and upper jaws, and perhaps the palatine in *Notelops*. This, and the rigidity between premaxilla and maxilla, suggest a feeding mechanism similar to large-mouthed salmonids.

V. SUMMARY

1. Osteological descriptions of *Notelops brama* (Agassiz), *Rhacolepis buccalis* Agassiz and *Pachyrhizodus* [=*Thrissopater*] *megalops* (Woodward) are given. The description of *Notelops brama* is only partial, because Dunkle (1940) has described much of the cranium of this species. Brief notes on the osteology of *Elopopsis*, as represented by *E. crassus* Dixon, are included. *Elopopsis* is thought to be related to *Pachyrhizodus* because of superficial similarities in the skull roof, the dentition, the opercular bones and the squamation at the base of the pectoral fin. Inadequate knowledge of *Elopopsis* precludes further discussion.

2. *Thrissopater* Günther is placed in synonymy with *Pachyrhizodus* Dixon as there is no justifiable basis for separation. The frontal depression, characteristic of *Thrissopater*, is known in *Pachyrhizodus* and the presence of an inner premaxillary tooth, characteristic of *Pachyrhizodus*, is strongly suspected in *Thrissopater*. The English species of *Pachyrhizodus* (including *Thrissopater*) are known mainly by jaw fragments and these species are rediagnosed using these criteria. Other species of *Pachyrhizodus* known from North America and Australia are comparable with the English species (particularly *P. subulidens* and *P. basalis*) in the features of the skull roof, circumorbital and opercular series and in the jaws.

3. *Notelops*, *Rhacolepis* and *Pachyrhizodus* form a monophyletic group, the suborder Pachyrhizodontoidei *nov.*, which is distinguished by features in the circumorbital series (lack of a separate antorbital, fusion between the second and third infraorbitals and the pattern of branching within the dermosphenotic) and the caudal skeleton (separate preural and ural centra, fusion of the parhypural with the first preural centrum, fusion of a compound lower hypural plate with the first ural centrum, a large first uroneural and, at least in *Rhacolepis*, a fusion of the first preural neural arch with the supporting centrum).

4. The combination of derived character states shown by the Pachyrhizodontoidei is most favourably compared to that seen in the Protacanthopterygii. These features are so widely distributed within the protacanthopterygians that it appears impossible to refer the pachyrhizodontoid fishes to any recognized suborder and therefore they must be separated from them at least at the subordinal rank. A general resemblance in features of the skull roof, jaws and vertebral column is noted between pachyrhizodontoids and the large-mouthed salmonids. The Protacanthopterygii and the Euteleostei are, at present, not defined and for this reason the suborder Pachyrhizodontoidei is classified as Teleostei *incertae sedis*.

5. Within the Pachyrhizodontoidei, *Rhacolepis* and *Pachyrhizodus* share several derived character states (e.g. loss of a bone-enclosed ethmoid commissure, separated parietals, loss of the subtemporal fossa and prootic–intercalar bridge, fusion of angular and articular and loss of gular plate) not seen in *Notelops*. *Rhacolepis* and *Pachyrhizodus* are therefore united in the family Pachyrhizodontidae. *Notelops* is placed in the family Notelopidae *nov.* and is considered to be the plesiomorph sister-group of the Pachyrhizodontidae. *Notelops* is probably derived with respect to *Rhacolepis* and *Pachyrhizodus* in showing an elongate, toothed palatine that functionally replaces the ectopterygoid.

VI. ACKNOWLEDGEMENTS

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VII. ADDENDUM

Since the preparation of the final draft of this manuscript, Taverne (1974) has published a paper which includes notes on the systematic position of *Notelops*. Taverne notes similarities and differences between *Elops* and *Notelops* and reaches the conclusion that *Notelops* should be placed in the Salmoniformes, in a new suborder Notelopoidei Taverne. He interprets *Notelops* as a form occupying a phylogenetic position intermediate between elopomorphs and euteleosts (Taverne 1974 : fig. 40).

I would agree with Taverne that *Notelops* shows features that suggest relationship with 'salmoniform' fishes but I fail to see the validity of his arguments. Further, I do not think it wise to place *Notelops* in the Salmoniformes.

Taverne notes that the differences between elopoids and *Notelops* are points of similarity with salmoniforms. Some of these so-called differences are not apparent in any of the specimens used in the preparation of this paper. Thus, two of the differences mentioned by Taverne are the lack of teeth upon the pterygoids and the lack of a buccohypophyseal canal in *Notelops*. All of the specimens of *Notelops* that I have examined show villiform teeth on the endopterygoid and the presence of a buccohypophyseal canal. Furthermore, certain of the differences mentioned by Taverne do not appear to be significant. Thus, Taverne mentions that *Notelops* differs from *Elops* in the presence of a pair of notches, just in front of the ascending wings of the parasphenoid, for the efferent pseudobranchial arteries. *Elops* is without these notches ; *Notelops* is variable as to whether the efferent pseudobranchial passed through a notch, a foramen or 'marked' the parasphenoid at all. Another difference mentioned by Taverne is the 'well-developed' supraoccipital crest contrasting with the very small crest in *Elops*. It is true that *Notelops* has a proportionately larger crest but the magnitude of the difference does not constitute a significant difference.

Taverne notes the presence of a 'fenêtre auditive' in *Elops*, reputedly absent in *Notelops* (and Salmoniformes). The 'fenêtre auditive' in *Elops* referred to by Taverne is a small triangular space left between the prootic, exoccipital, basioccipital and parasphenoid (Taverne 1974 : fig. 2, *f.b.s.*). In *Elops*, and indeed in the many other fishes which show this feature, the space is covered by membrane. A similar space is shown in some specimens of *Notelops* (Fig. 2, p. 132) and in many young individuals of recent salmonids and ostariophysans. Moreover, it is not present in all species of *Elops* (Forey 1973b : fig. 3). The presence of the gap appears to represent an ontogenetic stage, prior to the full growth of the surrounding bones. The choice of the term 'fenêtre auditive' by Taverne is unfortunate for it in no way represents an auditory fenestra such as is seen in clupeomorphs and *Hiodon*. In these latter fishes this auditory fenestra is between the basioccipital, exoccipital and prootic and is a large oval opening.

Taverne mentions four further differences between *Elops* and *Notelops*. In *Notelops* there are no teeth upon the parasphenoid, the saccular chamber is not inflated, an antorbital is absent and there is fusion between members of the infraorbital series. I agree with these differences but do not think that they show evidence of particular relationship with the Salmoniformes. It is true that these features are found, in sporadic fashion, within the Euteleostei. Taverne justifiably suggests that elopoids and Salmoniformes belong to the same broad phylogenetic lineage. However, Taverne argues that because *Notelops* differs (some of these 'differences' have been questioned above) from elopoids then *Notelops* must be placed in the Salmoniformes. No good reason is given for placing *Notelops* in the Salmoniformes rather than any other euteleostean group.

Finally, two features of *Notelops* reported by Taverne (1974 : 78) must be corrected. He says that the jaws are edentulous and that there are two supramaxillae. In fact, the premaxilla, maxilla and dentary bear many teeth (see also Woodward 1901, Jordan & Branner 1908, Dunkle 1940) and there is a single splint-like supramaxilla.

VIII. REFERENCES

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IX. ABBREVIATIONS USED IN FIGURES

Ang	angular
Ang-art	angulo-articular
Art	articular
Asp	autosphenotic
a.t.f.c	anterior opening of jugular canal
Bb	basibranchial (numbered 1–3)
$Bb.tp_{1+2+3}$	tooth plate associated with Bb_{1-3}
Boc	basioccipital
Br.r	branchiostegal ray
Bsp	basisphenoid
Cb	ceratobranchial (numbered 1–5)
Ce.a	anterior ceratohyal
Ce.p	posterior ceratohyal
Cl	cleithrum
Cor	coracoid
c.s	caudal scute
De	dermethmoid
Den	dentary
d.f	dilatator fossa
d.l	dorsal (epiotic) limb
Dsp	dermosphenotic
Eb	epibranchial (numbered 1–3)
e.com	ethmoid commissure
Ect	ectopterygoid
Enpt	endopterygoid
Ep	epural (numbered 1–2)
Epo	epiotic
Exo	exoccipital
fa.eth	facet for articulation with the ethmoid
fa.hm	facet for hyomandibular
fa.pal	facet for articulation with the palatine
fa.qu	facet for articulation with the quadrate
f.b.h.c	foramen for buccohypophyseal canal
f.e.p.a	foramen for efferent pseudo-spiracular artery
fh	foramen between H_1 and H_2
f.i.c.a	foramen for internal carotid artery
f.m	foramen magnum
f.m.c.v	foramen for middle cerebral vein
f.occ.n	foramen for occipital nerve
f.o.n.a	foramen for orbital artery
f.p.c	foramen for profundus ciliaris
f.p.f	foramen leading to post-temporal fossa
Fr	frontal
f.stt.com	foramen for supratemporal commissure
f.VII.hm	foramen for hyomandibular trunk of VII
f.VII.ot	foramen for otic branch of VII
H	hypural (numbered 1–4)
Hb	hypobranchial (numbered 1–4)
Hm	hyomandibular
Ib	infrapharyngobranchial (numbered 1–3)
Ic	intercalar
il.re	iliac region
Int	interhyal
Io	infraorbital (numbered 1–5)

Iop	interoperculum
io.s.c	infraorbital sensory canal
is.re	ischial region
L.e	lateral ethmoid
l.l.	lateral line
M.c	Meckelian cartilage
M.cor	mesocoracoid
Mpt	metapterygoid
Mx	maxilla
Na	nasal
NaPu	neural arch associated with preural centrum (numbered)
NsPu$_2$	neural spine associated with second preural centrum
Op	operculum
Ors	orbitosphenoid
Pa	parietal
Pal	palatine
Par	parasphenoid
Pcl.d	dorsal postcleithrum
Pcl.v	ventral postcleithrum
Ph	parhypural
Pmx	premaxilla
Pop	preoperculum
Pop.s.c	preopercular sensory canal
p.re	pubic region
Pro	prootic
Psp	pterosphenoid
p.t.f.c	posterior opening of jugular canal

Pto	pterotic
Ptt	post-temporal
Pu	preural centrum (numbered 1-4)
Qu	quadrate
Rad	radial (numbered 1-4)
Rart	retroarticular
S.Art	sesamoid articular
Sca	scapula
Scl	supracleithrum
Smx	supramaxilla
So	supraorbital
Soc	supraoccipital
Sop	suboperculum
so.s.c	supraorbital sensory canal
Stt.com	supratemporal commissure
Sy	symplectic
U	ural centrum (numbered 1-2)
Un	uroneural (numbered 1-3)
Ur	urohyal
v.l	ventral (intercalar) limb
Vo	vomer
I	foramen for olfactory tract
III	foramen for occulomotor
IV	foramen for trochlear
V	foramen for trigeminal
IX	foramen for glossopharyngeal
X	foramen for vagus

X. INDEX

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EVOLUTIONARY TRENDS IN SOME MESOZOIC TEREBRATELLACEA

E. F. OWEN

BULLETIN OF
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GEOLOGY Vol. 28 No. 3
LONDON : 1977

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EVOLUTIONARY TRENDS IN SOME MESOZOIC TEREBRATELLACEA

BY

ELLIS F. OWEN

Pp. 205–253 ; 3 *Plates* ; 29 *Text-figures*

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By E. F. OWEN

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SYNOPSIS

While the use of all morphological characters in the classification of the articulate brachiopods is desirable, it is suggested that more use could be made of the cardinalia in the border classification of some Cretaceous Terebratellacea. In this paper, some detailed features of the cardinal process in certain genera are used to demonstrate trends which are thought to have an evolutionary significance.

A systematic study is made of some of the costate Terebratellacea from the Cretaceous, some of which have not previously been assigned to subfamilies. Two new genera (*Helvetella, Ruegenella*) and three new species (*Ruegenella ciplyensis, Oblongarcula alemannica, Arenaciarcula acuticostata*) are described. Lectotypes are selected for *Gemmarcula menardi* (Lamarck) from the Cenomanian of Le Mans, France, and for *Trigonosemus elegans* Koenig from the Maastrichtian of Normandy.

I. INTRODUCTION

IDEALLY, the broader classification of any group of brachiopods to the level of family and subfamily depends largely upon interpretation of the greatest number of characters. In the fossil articulates, such characters have included shell structure, punctation, early and mature loop development, size and type of cardinal process and other aspects of the cardinalia, as well as external morphology, folding, general outline and ornament.

Of these, perhaps the most important for the classification of the Terebratellacea has been the pattern of early stages in the development of the brachial loop. The work of Elliott (1947, 1950, 1953) now allows a better understanding of these patterns; his descriptions and illustrations of the ontogenetic development of loops of *Hamptonina*, from the Upper Jurassic, and *Gemmarcula*, from the Upper Aptian, have been one of the chief sources of reference in the classification of fossil Terebratellidae and Dallinidae for several years.

Baker (1972) demonstrated a similar ontogenetic series, using reconstructions from transverse serial sections and dissections of minute individuals of the zeilleriid *Zeilleria leckenbyi* from the Jurassic of the Cotswolds. His work confirmed, in many ways, the views of Babanova (1965) who found that, in certain species of *Aulacothyris* from the Jurassic of the Soviet Union, there was a connection between the loop and median septum in the early stages of ontogeny. Baker also demonstrated very convincingly that, during the early ontogenetic stages of *Z. leckenbyi*, both terebratellid and dallinid characteristics are visible.

The reliability of methods such as those employed by Elliott (1947, 1950) in the determination to family and subfamily level depends to a great extent upon the availability of suitable young forms which can be dissected. Within the Mesozoic, however, the difficulties in determining such early differences in loop development are well known. Baker (1972) overcame a great many of these in his approach to *Z. leckenbyi* by using a number of carefully selected young stages. Unfortunately such stages are not common among Mesozoic collections, in many cases the only specimens available for study being already mature.

An alternative approach to this problem, although by no means a replacement, can be made in some genera and species through a more critical and detailed study of the general morphological features and relative size of the cardinal process. Cooper (1970), in a review of generic characters in brachiopods, has stressed the importance of the cardinal process in defining genera, particularly in early Palaeozoic forms. He also pointed out (1970 : 230) that Mesozoic terebratulids and terebratellids had a similar development of cardinal process. The present study draws upon Cooper's ideas that greater use of this structure, and a broader understanding of the cardinalia generally, may help in defining genera – or at least in increasing our knowledge of all the characters available for classification.

Within certain Palaeozoic suborders of brachiopoda, such as the Productidina and Chonetidina, the cardinal process has been used to advantage in broader family classification. Muir-Wood & Cooper (1960) recognized at least eight distinct morphological types within the Productidina alone, distinguishing the various types mainly on the general outline of the external face of the process, the presence or absence of a supporting median septum and the number of lobes constituting the boss.

The Mesozoic Terebratellacea examined here present less of a problem since fewer morphological varieties exist. Within the Cretaceous, three main morphological features of the cardinal process appear to predominate. One of these is the flattened, shallow, disc-like structure observed in *Oblongarcula* (Fig. 15, p. 230) which is certainly a poorly-developed structure not always clearly defined in transverse serial sections. It nevertheless appears to be more than just a mere flattening of the posterior end of the brachial valve and must surely have been functional.

Secondly, a more highly developed cardinal process of type similar to that just described is represented by the genus *Arenaciarcula* (Fig. 20, p. 237). Here the disc-like structure has been partially divided by indentations at approximately midway along its posterior and anterior walls, producing a bifid process.

A shallow disc-like structure is also observed in *Gemmarcula*, but in this genus the lateral rims of the process are more highly developed than in *Oblongarcula* or *Arenaciarcula* and can be recognized in transverse serial sections as two inwardly-curving plates which project a short distance into the umbonal cavity of the pedicle valve (Fig. 2, p. 212). This type of cardinal process can be seen to develop into a short, tube-like structure as seen in dissections of *G. canaliculata* (Fig. 6, p. 217) and *G. carantonensis* (Fig. 7, p. 218). The structure becomes grossly thickened in *G. carantonensis* but can still be recognized in serial sections as two distinct inwardly-curving plates (Fig. 8, p. 219).

The third main type of cardinal process observed within the Cretaceous is represented by *Dereta*, *Terebrirostra* and *Trigonosemus*. Although each of these can be clearly differentiated by generic characters which include some aspects of the cardinalia, in the main the massive cardinal boss supported by the high persistent septum and the elongate fused hinge-plates extending well into the pedicle umbonal cavity are conspicuous characters common to all three. In *Terebrirostra* and *Trigonosemus*, however, the cardinal process appears to develop three lobes which can be clearly seen in transverse serial sections (Fig. 23, p. 241 and Fig. 28, p. 247) whereas in *Dereta* (Fig. 29, p. 248) only two lobes can be recognized.

II. EXTERNAL MORPHOLOGY

FOLDING. The type of folding and sulcation of the anterior commissure seen throughout the range of genera and species of Terebratellidae examined falls within well-marked limits. These are *rectimarginate*, *uniplicate*, *intraplicate* and *antiplicate*.

No strong genetic link affecting the form of the anterior commissure is suggested, but it is felt there is some influence affecting the basic pattern of this character which is recognizable in succeeding genera within any given stock, albeit changed or modified by ecological conditions.

Cooper (1970 : 205) suggested that folding had seldom been used as a principal factor in generic definition. As a general rule this is so, but more importance is attached to it in the study of Terebratellacea described here. Similarity of folding may not prove of any consequence considered alone, but could be an additional guide in relating genera and species within a subfamily.

In the Upper Jurassic and Lower Cretaceous, intraplicate and antiplicate commissures occur within stocks of Terebratellacea which appear to have other characters in common. One of these is represented by *Ismenia pectunculoides* (Schlotheim) (Pl. 2, figs 3a–c) from the Upper Jurassic of Germany. The intraplicate commissure, transverse lamellar ornament and radial costae are strongly-developed characters which also occur in *Gemmarcula aurea* Elliott from the Upper Aptian and other related species within the Albian and Cenomanian. These features can also be recognized in *Ruegenella humboldti* (Hagenow) from the Maastrichtian of north Germany, which is believed to be directly related to *Gemmarcula* but to have evolved beyond the generic range of that form.

COSTATION. Shell ornament is very variable, not only from one species to another but also within the recognizable range of a given species. In general, the range includes ornament of strong, deeply-incised costae, such as those of *Arenaciarcula acuticostata*, to fine, frequently bifurcating, rounded costae as found in *Trigonosemus elegans*. In spite of a wide degree of variation most costae or costellae conform to a broad generic pattern. In the case of *Oblongarcula*, for example, costae tend to be fairly sharp or angular, varying mainly only in degree of coarseness.

Additional ornament of transverse lamellae occurs in some genera such as *Gemmarcula*, and is more marked on the surface of some species. It is possible that this character is largely affected by environmental change, as some individuals within a specific range show considerable degrees of variation from very faint to almost rugose.

Bifurcation of costae appears to be more common in some species than others and intercalation, which is a rare occurrence in the Cretaceous Terebratellacea, can also be seen in certain well-marked species.

EXTERNAL OUTLINE. Surlyk (1972), discussing the morphological adaptation of brachiopod faunas within the Danish Upper Chalk, grouped various genera and species according to their ecological habits. Some of the forms which he grouped as 'living free on the substrate' (Group II) were seen to assume the same or similar morphological characters. Of his 'hemispherical free living species', '*Gemmarcula*' *humboldti* and *Trigonosemus pulchellus* are discussed in the systematic section of this paper.

The degree of incurvature of the beak and the convexity of the valves are also important. This can be illustrated here, particularly within the Gemmarculinae, which have a broad range of ecologically-controlled umbonal patterns ranging from massive, truncated by large foramen, to slightly-produced suberect, with small foramen. This reflects the environment of the fauna.

III. SYSTEMATIC DESCRIPTIONS

Family **DALLINIDAE** Beecher 1893

Subfamily **GEMMARCULINAE** Elliott 1947

Genus ***GEMMARCULA*** Elliott 1947

[= *Trifidarcula* Elliott 1959]

Type species. *Gemmarcula aurea* Elliott 1947.

Description. Since the original description of the genus by Elliott (1947), transverse serial sections have been made of the type species *G. aurea* from the Lower Greensand, Faringdon, Berkshire. These confirm the original diagnosis and description of the cardinalia and loop of the adult form and are presented here in Fig. 2.

Remarks. A series of ontogenetic stages in the development of the brachial loop of *G. aurea* was demonstrated by Elliott (1947) which showed the pre-campagiform and campagiform stages to perfection. Barczyk (1969 : 12) showed a similar series of dalliniform stages in the development of *Ismenia pectunculoides* (Schlotheim) from the Upper Jurassic, Holy Cross Mountains, Poland. Externally the two genera have much in common with similar intraplicate folding of the commissure and general outline. The transverse shell ornament of evenly-spaced lamellae in addition to the radiating costae is also a feature of both forms. This is more apparent in *Gemmarcula trifida* (Meyer) (Pl. 1, figs 4a–c) and *G. pterygotos* (Walker) (Pl. 2, figs 1a–c, 2a–c).

It is possible that *Gemmarcula* has, in the general course of brachiopod evolution, been developed directly from *Ismenia*, but intermediate forms which may link them or, at any rate, bring them closer together, have not yet been investigated.

Gemmarcula aurea Elliott 1947

Figs 1, 2 ; Pl. 1, figs 3a–c.

1826 *Terebratula truncata* J. de C. Sowerby (*non* Linné) : 71 ; pl. 537, fig. 3.
1852 *Terebratula menardi* (Lamarck) ; Davidson : 24–26 ; pl. 3, figs 34–39, 41.
1874 *Terebratula truncata* (Sow.) ; Davidson : 25.
1947 *Gemmarcula aurea* Elliott : 146 ; pls 3, 4, figs 1–33.

Emended description. The fourteen transverse serial sections given in Fig. 2 show the minor development of the cardinal process, the short divergent dental lamellae and the shallow hinge-trough buttressed by the stout, low median septum. They also show the rather poor development of the hinge-plates and the relative persistence of the supporting median septum.

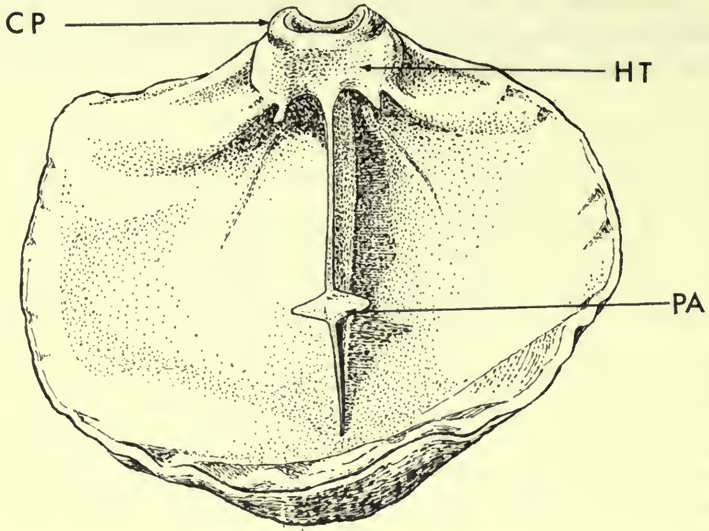


Fig. 1. Drawing of a dissected brachial valve of *Gemmarcula aurea* Elliott from the Upper Aptian, Faringdon, Berkshire. The simple cardinal process CP consists of a thickened disc-like depression at the posterior extremity of the broad, shallow hinge-trough HT. The point of attachment of descending branches of the brachial loop PA appears low on the high, persistent median septum. × 4.

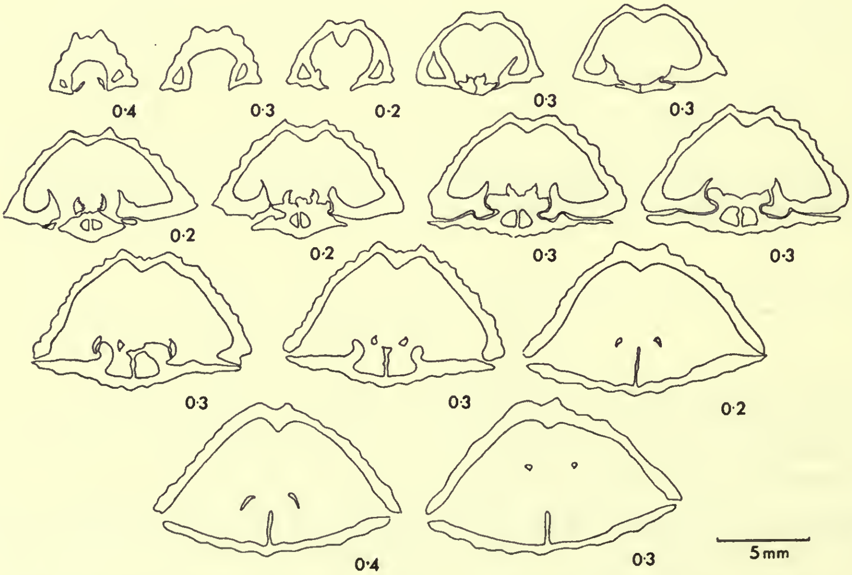


Fig. 2. A series of 14 transverse serial sections through the umbo of a specimen of *Gemmarcula aurea* Elliott, showing the comparatively short dental lamellae, simple bifid cardinal process, fused hinge-plates and high supporting median septum.

The point of attachment of descending branches to the septum has not been shown in serial sections here as this occurs beyond the mid-line of the brachial valve and is often damaged in individuals from the type locality. Nevertheless, this feature has been adequately described and figured by Elliott (1947).

The flaps or septal flanges described by Elliott (1947 : 150) occurring on the lateral extremities of the transverse band of the brachial loop in mature forms of *G. aurea* are not now considered to be of subfamily importance (Elliott 1957 : 336); they are probably caused by supplementary calcification from early developmental stages which became part of the loop when persisting to the adult stage. This view is confirmed by Richardson (1975 : 294), in a brief review of their general significance.

Atkins (1959 : 421) compared these structures to similar horn-like projections on the transverse band in early loop stages of the Recent *Terebratalia transversa* (G. B. Sowerby) but, unlike those of *Gemmarcula*, these structures are not maintained in the adult stages.

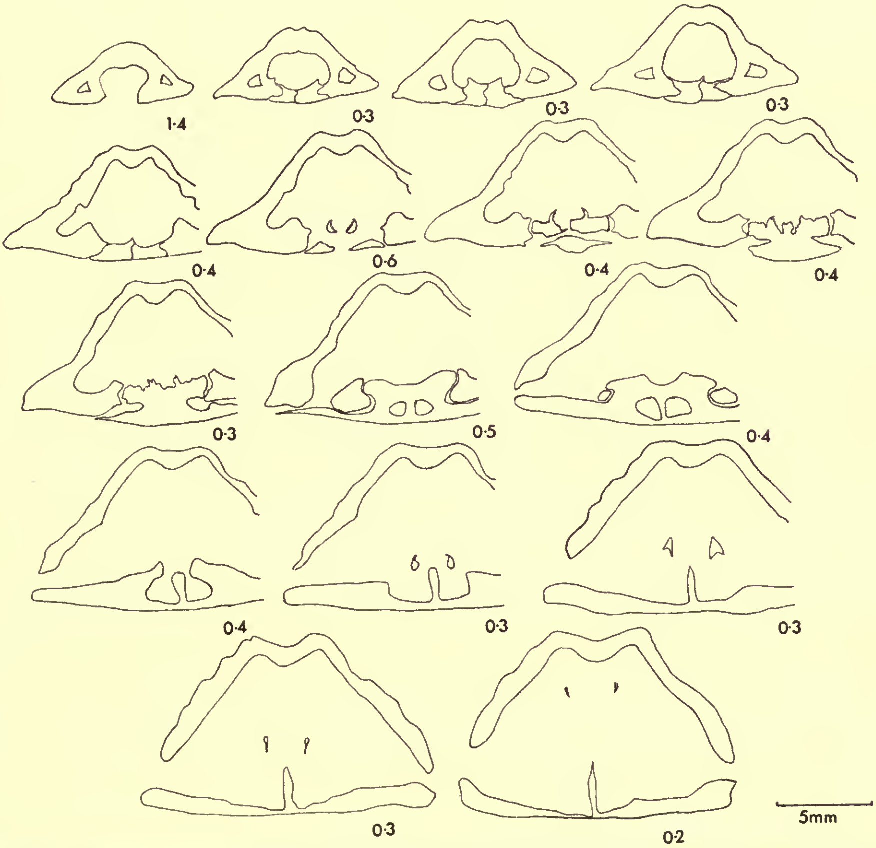


FIG. 3. Transverse serial sections through a specimen of *Gemmarcula pterygotos* (Walker) from the Lower Albian, Munday's Hill, Leighton Buzzard, Bedfordshire, showing the same generic features as the type species *G. aurea* Elliott.

Steinich (1965) used these structures as points of distinction when he assigned '*Terebratella*' *humboldti* Hagenow from the Rügen Chalk, Maastrichtian of north Germany, to the genus *Gemmarcula*. A more critical examination of the cardinalia of specimens of '*T.*' *humboldti* from the Rügen Chalk by both Finn Surlyk and myself has revealed that, although there is an undoubted relationship between '*T.*' *humboldti* and *Gemmarcula aurea*, it is not as close as Steinich suggested. A comparative study of certain fundamental differences in the cardinalia is discussed below in the description of *Ruegenella* gen. nov., to which '*T.*' *humboldti* has now been assigned.

Holotype. The specimen figured by Elliott (1947 : pl. 3, figs 8–10) is housed in the British Museum (Natural History) and registered as BB 9251.

Horizon and Locality. *Gemmarcula aurea* Elliott has not been recorded outside the Lower Greensand of Britain, where it appears to be confined to the Sponge Gravel of Faringdon. A species which approaches it in general morphology is *G. crassicosta* (Leymerie) from the Lower Cretaceous of Vimport, France. This was recently the subject of papers by Calzada (1975, 1976) with accompanying serial sections.

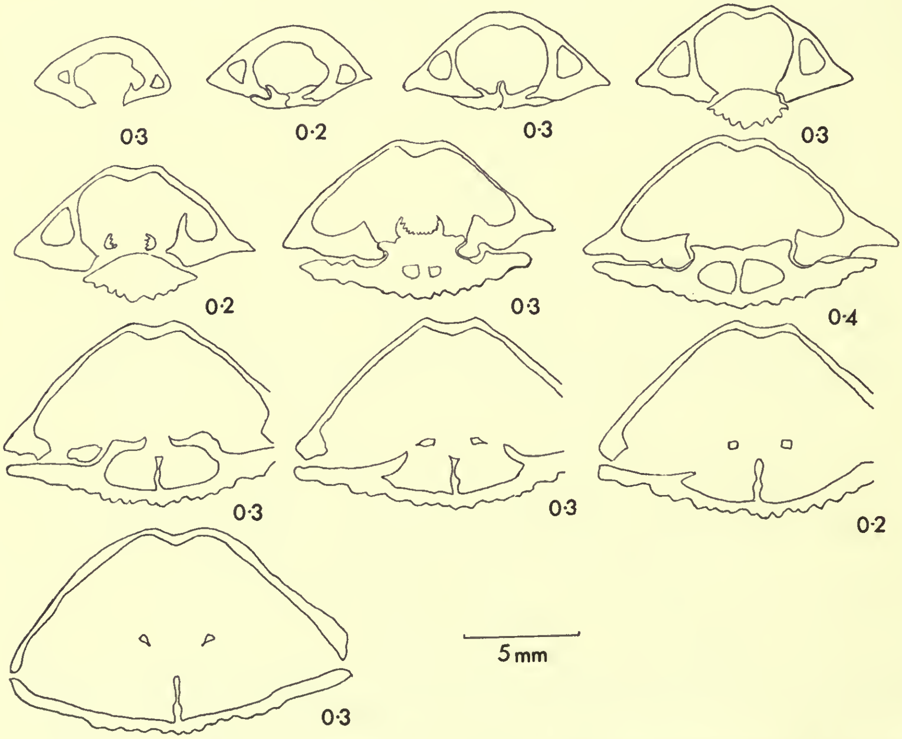


Fig. 4. Eleven serial sections through a specimen of *Gemmarcula asteriana* (d'Orbigny) from the Aptian of La Clape, France, confirming Elliott's original assignment of this species to *Gemmarcula*. (See also Pl. 1, Fig. 6 and Pl. 2, Fig. 9.)

Gemmarcula menardi (Lamarck 1819)

Fig. 5 ; Pl. 1, figs 2a–c.

1819 *Terebratula menardi* Lamarck : 256, no. 50.
1834 *Terebratula menardi* Lamarck ; von Buch : 78 ; pl. 3, fig. 42.
1838 *Terebratula menardi* Lamarck ; von Buch : 184 ; pl. 17, fig. 6.
1848 *Terebratella menardi* d'Orb. ; d'Orbigny : 118 ; pl. 517, figs 1–15.
1852 *Terebratella menardi* Lamarck ; Davidson : 24 ; pl. 3, fig. 42.
1867 *Terebratella menardi* Lamrk. ; Schloenbach (partim) : 458 ; pl. 22, fig. 1.
1871 *Terebratella menardii* Quenstedt : 261 ; pl. 517, figs 1–15.
1918 *Terebratula menardii* (Val. in Lam.) ; Favre : pl. 16, figs 93–99.
1947 *Gemmarcula menardi* (Lamarck) Elliott : 154.
1955 *Gemmarcula menardi* (Lamarck) ; Cooper : 10, pl. 2B, figs 29–34.

EMENDED DESCRIPTION. In view of the accompanying transverse serial sections and other information obtained from comparative material, it is thought necessary to give a brief emendation to the descriptions so far available.

Elliott (1947 : 154) pointed out that the chief differences between the Cenomanian *G. menardi* and the type species *G. aurea* were that, in the Cenomanian form, the general width was proportionately greater and that the costae were clearer-cut or more acutely incised. It may be added that in *G. menardi* the median fold on the brachial valve is usually better developed or more marked, the interarea more extensive and the foramen considerably smaller than in the Aptian species *G. aurea*. Elliott also remarks that the cardinalia are similar, though the adult septum is longer in *G. aurea*. This observation is confirmed in the serial sections shown here, Fig. 5. In addition, the cardinalia are, if anything, slightly more advanced in development in the adult *G. menardi*, the posterior part of the hinge-trough occupied by an anteriorly thickened cardinal process. Fundamentally the arrangement of the cardinalia, the type of cardinal process and the shape of the hinge-trough are very much the same in both species.

LECTOTYPE. Of the eleven syntypes in the Lamarck Collection, Muséum d'Histoire Naturelle, Geneva, the seven best-preserved (A–G) were figured in the catalogue of the Lamarck Collection by Favre (1918). The specimens are labelled as from 'Coulaines, près du Mans' and, from the preservation and matrix, are probably of Middle Cenomanian age from the well-known locality at Le Mans, Sarthe, France. The specimen selected here as lectotype of the species is the specimen labelled 'A' in the Lamarck Collection and figured by Favre (1918 : pl. 16, figs 93a–d).

DIMENSIONS. Lectotype 9·5 mm long, 12·0 mm wide and 6·2 mm thick. Other specimens, all from the type locality and housed in the British Museum (Natural History), London, have dimensions as follows (measurements in mm).

	Length	Width	Thickness
B 5156	13·0	18·2	9·9
	15·0	16·0	9·0
	12·7	14·5	6·4

	Length	Width	Thickness
65685	15·9	14·0	10·0
	13·0	14·0	10·0
	12·5	15·4	8·9
	12·9	15·6	8·0
	14·0	13·1	8·5
	11·5	13·9	7·9

Distribution. Apart from the type locality (at Le Mans, Sarthe, France) the species has been recorded from the Middle Cenomanian of Essen, north Germany,

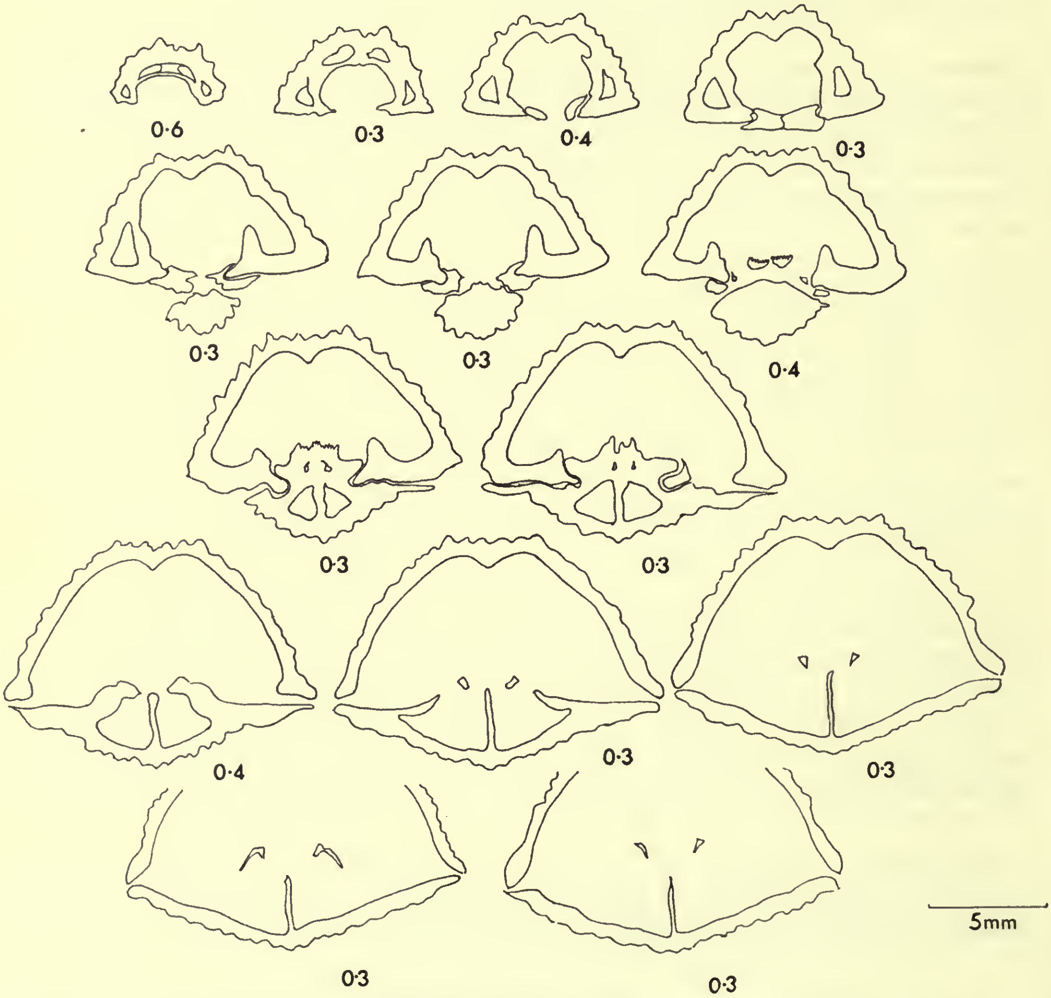


Fig. 5. Serial sections of *Gemmarcula menardi* (Lamarck) from the type locality of Le Mans, Sarthe, France. These show a slightly more highly developed cardinal process than is seen in the type species, and thickened cardinalia and lining-plates.

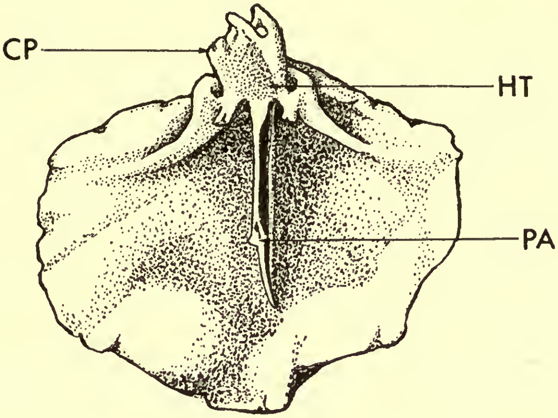


Fig. 6. Dissected brachial valve of a specimen of *Gemmarcula canaliculata* (Roemer) from the Tourtia of Tournai, Belgium, showing the extreme development of the cardinal process CP in this species. × 8.

the Tourtia of Tournai, Belgium and from the Middle Cenomanian of Dorset, Wiltshire and the Isle of Wight, England.

Remarks. Among the ecological variants which have been assigned to this species are two forms described from the Cenomanian limestones of Poland. These are discussed in the remarks under *G. hercynica.*

The species described by d'Orbigny (1848 : 122) as *Terebratella carantonensis* is probably a further development or ecological variant of the type species. It occurs in the more chalky facies of the top beds of the Cenomanian in the Charente and Sarthe of northwestern France and bears most of the characters of the genus. It differs, however, in having a finer ornament of costae, less well marked median fold on the brachial valve and a less pronounced sulcus in the pedicle valve. The internal characters as seen in transverse serial sections, Fig. 8, show the same characteristic cardinalia and loop development as in the type species but also considerable secondary thickening, which makes these features difficult to recognize.

Gemmarcula menardi can be distinguished from *G. aurea* in having a wider hinge-line, more marked brachial fold and pedicle sulcus and sharper and more deeply incised radiating costae. It differs from *G. trifida* (Pl. 1, figs 4a–c) in having a less acutely developed median fold in the brachial valve and a greater number of clearly-defined radiating costae and shorter, or less extensive, interarea.

Gemmarcula carantonensis (d'Orbigny 1847)

Figs 7, 8 ; Pl. 1, figs 1a–c.

1848 *Terebratella carantonensis* d'Orbigny : 122 ; pl. 518, figs 1–4.

Emended description. Large subquadrate *Gemmarcula*, almost equally broad as long. Shell with faint brachial fold and fairly well-marked pedicle sulcus originating from the umbonal regions. Anterior commissure antiplicate, similar to that of *G. menardi*. An ornament of 36–40 rounded radiating costae, with frequent marginal bifurcation, adorns both valves, six or seven costae occurring on the fold with a corresponding number in the sulcus. The umbo is massive with distinct beak-ridges bordering an extensive interarea. A comparatively small, circular, submesothyridid foramen dominates a slightly incurved beak.

Distribution. d'Orbigny (1848) described the species from a level, now the *A. mantelli* Zone, of the Cenomanian from Port des Barques in the Charente. It was also stated to have been found at Eoux (Basses-Alpes). More recent records, particularly those of Kennedy & Juignet (1973), extend the geographical range to Cenomanian localities within Sarthe.

Remarks. It is with certain misgivings that this species is assigned to the genus *Gemmarcula*, since the internal structures as seen in both dissections and transverse serial sections depart slightly from the typical *Gemmarcula aurea* and *G. menardi*. After a great deal of consideration these comparatively minor differences, which amount to a more advanced cardinal process and considerable thickening of cardinalia, hinge-plates and septum, are now thought to be of secondary development. Nevertheless, the species does show some advancement towards another stage in the evolutionary range of the genus. It is therefore regarded as the ultimate representative species within this range.

d'Orbigny's original description was accompanied by an illustration (pl. 518, figs 1–4) which shows a specimen subcircular in outline with a suberect beak, extensive interarea and numerous strong costae with occasional bifurcation. I have examined over twenty specimens from the Charante and Sarthe but all have a

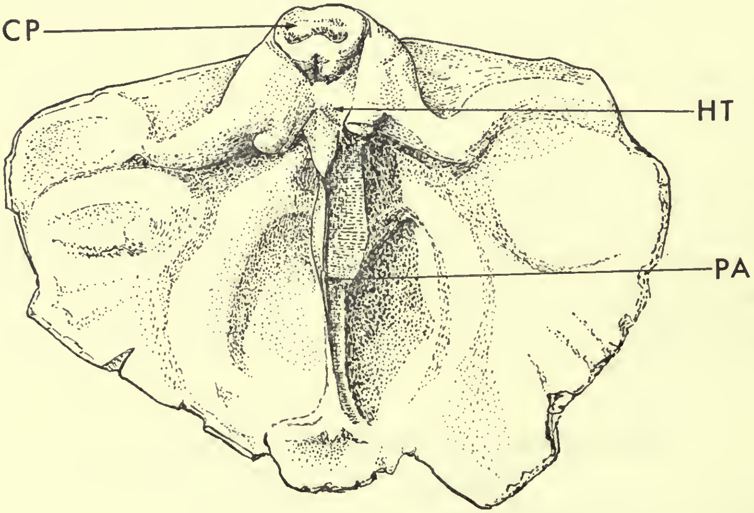


Fig. 7. The same generic characters are visible in this dissection of *Gemmarcula carantonensis* (d'Orbigny) from the Port des Barques, Charente, France, as appear in the type species, but are grossly thickened and difficult to differentiate. The hinge-trough HT, which is shallow, is not so clearly defined as in *G. aurea*. ×3.

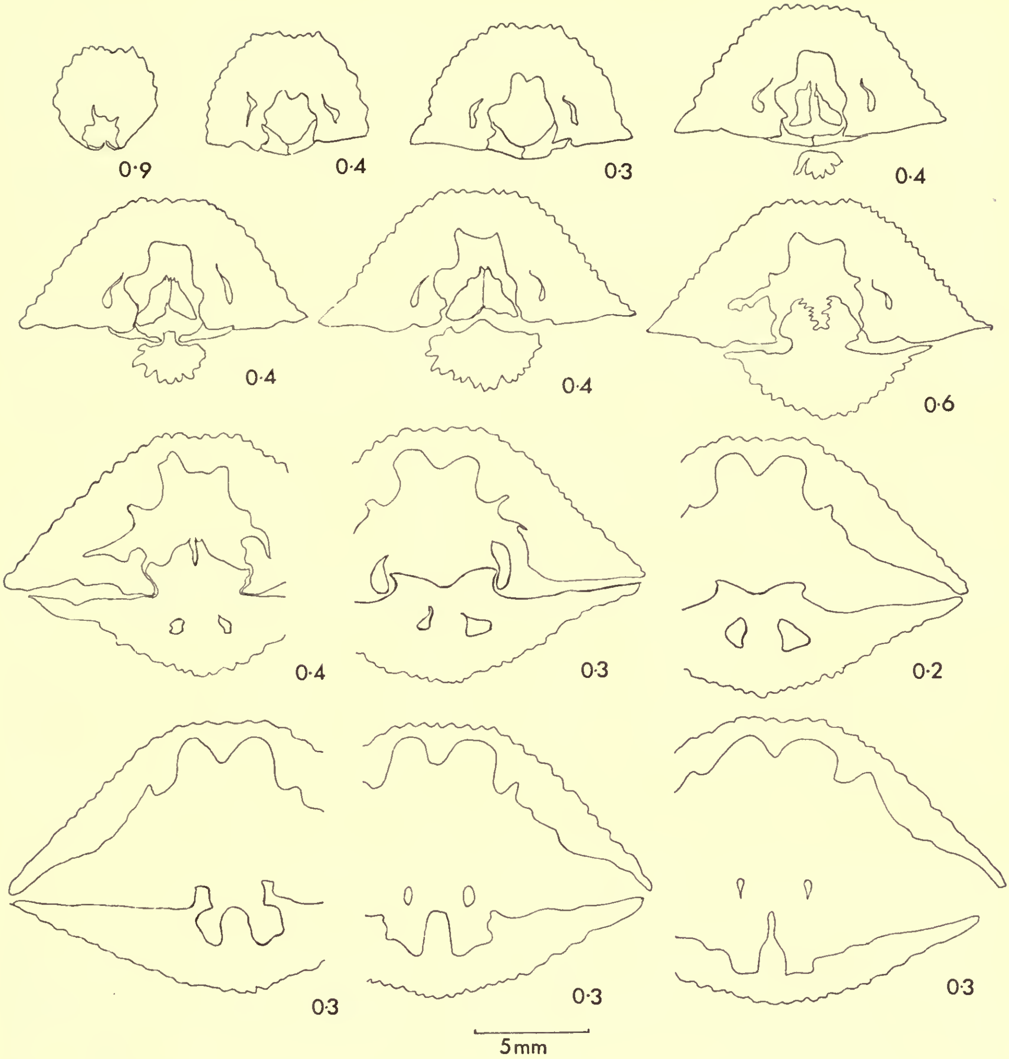


FIG. 8. Transverse serial sections of *Gemmarcula carantonensis* (d'Orb.), showing the secondary thickening of the vales and cardinalia, but the general characters can still be recognized.

more extended hinge-line than the one shown in d'Orbigny's figure. The beak characters are very much more variable than stated in the original description and the costae tend to be substantially finer, although this is a somewhat more variable character.

The species has been regarded as a reliable horizon marker within the Chalk, although at what particular horizon was not at all clear. Arnaud (1877 : 9–10), in his classic description of the Chalk of northwest France, suggests that *Terebratella* *carantonensis* characterizes a zone within the Turonian and quotes it in association with *Ostrea carinata*, *Hemiaster leymerei* and *H. verneuili*, etc.

Kennedy & Juignet recently reviewed the existing correlation of the Cenomanian/Turonian boundary in northern France and England. Their conclusions are tabulated (1973 : 196) in a revised correlation equating the Craie à *Terebratella carantonensis* with the lower part of the Melbourne Rock in southeast England and part of the fauna of the *Neocardioceras* Pebble Bed at the base of the Middle Chalk in Devon. From their analysis it seems that *G. carantonensis* occurs in the Upper Cenomanian.

DIMENSIONS. All material in the British Museum (Natural History), London. Figured specimen, BB 45960, 19·8 mm long, 20·0 mm wide and 10·5 mm thick. Other specimens have dimensions as follows (measurements in mm).

	Length	Width	Thickness
(a), from the Craie Chloritée, Charente, France			
B 6669	25·6	25·1	15·7
	21·5	21·1	11·4
	19·0	19·1	9·8
(b), from the Craie à *Terebratella carantonensis*, Port des Barques, Charente, France			
BB 45982	23·7	23·6	12·9
BB 45983	20·9	24·0	11·0
BB 45984	18·9	18·1	8·4
BB 45985	17·0	17·0	8·9
BB 45986	18·5	18·1	9·0

Gemmarcula hercynica (Schloenbach 1867)

1867 *Megerleia* (?) *hercynica* Schloenbach : 467 ; pl. 22, figs 6, 7.
1869 *Terebratella kurskensis* Hofman : 24 ; pl. 5, figs 12–15.

DESCRIPTION. Schloenbach's original description (1867 : 467) is adequate for the species, which is here referred to the genus *Gemmarcula* largely on account of external morphological similarities. The chief differences between *G. hercynica* and *G. menardi* appear to be confined to the hinge-line and costation. In *G. hercynica* the hinge-line is narrow and the interarea remains as a small triangle just anterior to the pedicle umbo. There appear to be two to three main costae radiating from either side of the main brachial fold, with faint costellae between each of the main costae.

REMARKS. Since the original description of this species under the name of *Megerleia* (?) *hercynica*, few references have been made to this form. The whereabouts of the two specimens figured by Schloenbach (1867 : pl. 22, figs 6, 7) is unknown and the question of proposing a neotype may have to be considered in due course.

Nevertheless, the species is well founded and easily distinguishable. Subsequent British and continental authors have described species referable to *Gemmarcula* which have a similar morphology to *G. hercynica* ; some of these are discussed here. One of them includes a specimen described and figured by Hofman (1869 : 24 ; pl. 5, figs 12–17) as *Terebratella kurskensis* from the Cenomanian of Russia which is here considered to be a synonym of *G. hercynica.* The narrow hinge-line costation and marked median brachial fold with flanking costellae suggest a very close relationship.

Confusion with Schloenbach's *G. hercynica* has arisen over a terebratelloid described by Walker (1903 : pl. 18, fig. 3) as *Terebratula menardi* var. *pterygotos* (Fig. 3, p. 213 ; Pl. 2, figs 1a–c, 2a–c). It is from the Lower Albian limestone of Shenley Hill, Leighton Buzzard, Bedfordshire, and is here referred to *Gemmarcula.* Though somewhat similar in general outline and morphology, it differs from *G. hercynica* (Schloenbach) in having a much more extensive hinge-line and interarea. It is generally broader and has more consistently even costation, but there appears to be a considerable range of variation within the species.

A species approaching *G. hercynica* in external morphology was described and figured by Ravn (1925 : 24 ; pl. 1, figs 1a–d) as *Terebratella kofoedi* (Pl. 2, figs 4a–c) from the Cenomanian basal conglomerates of Bornholm, Denmark. It is somewhat narrower than either of the two specimens figured by Schloenbach and has three distinct ribs on either side of the central brachial fold. Although the internal structures of this form are unknown, it is considered referable to the genus *Gemmarcula.*

The specimen from the Cenomanian of Saratovsk, Russia, figured by Sintsov (1872 : pl. 13, figs 16, 17) as *Terebratella menardi* is not typical of the species and in many ways resembles Schloenbach's *T. hercynica.* It has more radial costae and slightly more prominent growth-lines, but in general outline the two forms are very much alike.

Sintsov's specimen also resembles the specimen figured by Panow (1969 : 589, pl. 112, fig. 4) from the Cracow district of Poland, although the latter appears to have been an internal mould and does not show the radiating costae to advantage. In general outline Panow's specimen resembles one figured by Popiel-Barczyk (1972 : pl. 1, fig. 6) from the Cenomanian of Annapol, Russia, except that it is broader and has a more acute fold on the brachial valve. None of the forms mentioned above is typical of the species described as *Terebratella hercynica* by Schloenbach and it is possible that they represent distinct subspecies of either *G. menardi* or *G. hercynica.*

Genus ***HELVETELLA*** nov.

TYPE SPECIES. *Terebratula* (*Terebratella*) *arzierensis* de Loriol 1864.

DIAGNOSIS. Pentagonal, uniplicate to parasulcate, evenly biconvex, costate Terebratellidae. Maximum width just posterior to mid-line. Umbo massive, beak suberect. Foramen large, circular, mesothyridid. Interarea extensive, slightly concave ; beak ridges distinct. Hinge-plates short, triangular, ventrally deflected. Symphytium short, broad. Cardinal process absent.

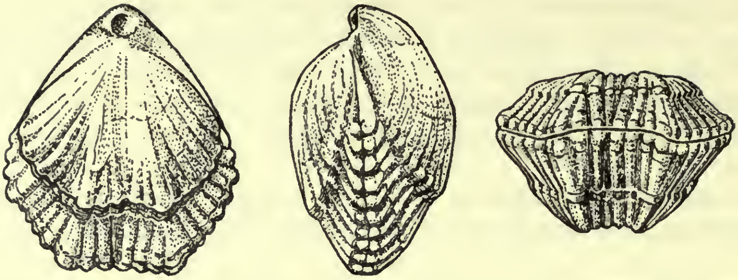


FIG. 9. *Helvetella arzierensis* (de Loriol), from the Valanginian of Arzier, Switzerland, showing the typical pentagonal outline, arrangement of costae and step-like growth lines. × 2.

Helvetella arzierensis (de Loriol 1864)

Figs 9, 10; Pl. 2, figs 5a–c.

1864 *Terebratula* (*Terebratella*) *arzierensis* de Loriol: 441; pl. 1, figs 11–13.
1866 *Terebratula* (*Terebratella*) *arzierensis* de Loriol; Schloenbach: 372.
1868 *Terebratula* (*Terebratella*) *arzierensis* de Loriol; de Loriol: 55; pl. 5, figs 2–5.
1872 *Terebratula* (*Terebratella*) *arzierensis* de Loriol; Pictet: 123; pl. 207, figs 3–6.

EMENDED DESCRIPTION. Although broadly pentagonal in general outline, the species is variable in form, ranging in length from 14 to 19·5 mm and in width from 11 to 18·5 mm. It has a generally somewhat terebratuloid aspect, but with numerous strong, bifurcating, rounded costae. The dichotomy of the costae is more evident nearer the margins. A fine, lamellar transverse ornament is noticeable, as well as one to three stronger concentric growth-lines which appear at about midway and just anterior of the mid-line in mature specimens.

A shallow sulcus originating from the pedicle umbo continues anteriorly, broadening at the margins. A similar, but shallower, sulcus is sometimes seen on the median fold of the brachial valve, but this is not regarded as a marked specific character. The sulci are often bounded by faint carinae in both valves.

Internal structure. As seen in successive serial sections, the short convergent dental lamellae soon diminish. No cardinal process is developed but a faint, cup-like, shallow hinge-trough, buttressed by a high, strong median septum, is deflected ventrally, giving rise to two triangular hinge-plates. The supporting median septum diminishes rapidly leaving extensive curved inner socket-ridges. These become more rectangular in outline, developing into the crural bases which in turn thin out to become well-developed crural processes. Finally, the descending branches of the brachial loop develop anteriorly, assuming what is thought to be a terebrataliform loop.

MATERIAL AND DIMENSIONS. It is not known for certain whether the specimen figured by de Loriol (1864: pl. 1, figs 11–13) is still extant. The question of selecting a lectotype from the two syntypes figured by de Loriol must, therefore, remain until exhaustive enquiries have been made. The specimen figured here, Pl. 2, figs 5a–c, is a topotype specimen in the Davidson Collection in the British

Museum (Natural History), BB 61527. The Davidson and general collections also contain eleven more topotypes, the dimensions of which are given below (measurements in mm).

	Length	Width	Thickness
BB 61527	18·0	16·0	11·0
B 6185	18·5	16·0	9·9
	19·9	18·1	10·1
	17·1	17·0	9·1
	15·2	13·2	8·8
	14·0	14·9	7·1
	13·1	13·7	6·2
	14·7	12·8	8·5
	12·1	10·8	6·1
B 35678	20·0	17·2	12·5
	14·0	14·9	7·4
	13·4	13·8	6·7

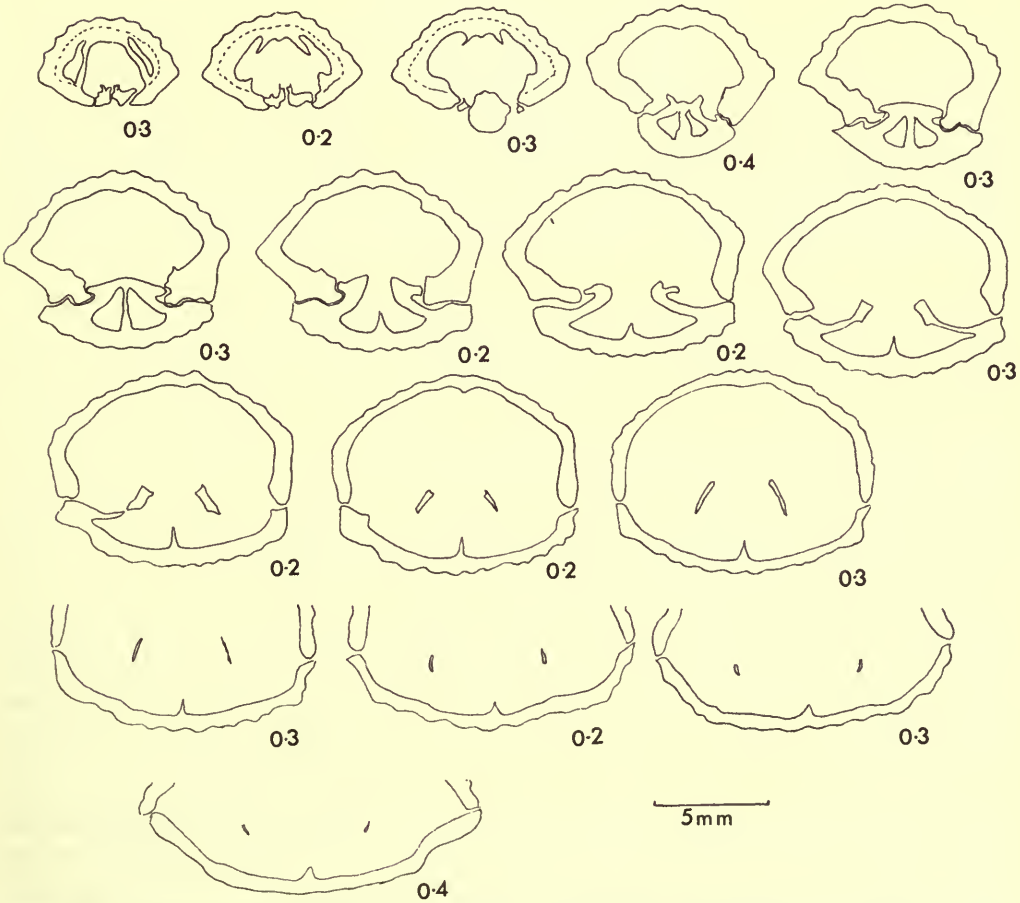


Fig. 10. Serial sections through a specimen of *Helvetella arzierensis* (de Loriol). The short dental lamellae are seen in the pedicle umbo and no cardinal process is developed.

Distribution. The type species, *Helvetella arzierensis* (de Loriol), is known only from the area of its original description, Arzier, Vaud, Switzerland, where it occurs in the Upper Valanginian of the Lower Cretaceous. Two other species are here referred to *Helvetella*, *Terebratella marini* and *T. riosi*, both described from the Valanginian of Valencia, Spain, by Bataller (1947).

Remarks. In general outline, folding and sulcation of the valves, *Helvetella arzierensis* has much in common with *Gemmarcula asteriana* (d'Orbigny) (Fig. 4; Pl. 1, figs 6a–c ; Pl. 2, figs 9a–c), which was originally described from the Aptian of Wassy and St Dizier (Haute-Marne), France. It differs in having coarser, more rounded costae, more step-like concentric growth-lines and different internal structure. Unlike *Gemmarcula*, *Helvetella* does not develop a cardinal process and the hinge-plates in the type species are developed directly from a ventrally deflected and shallow hinge-trough.

Genus ***RUEGENELLA*** nov.

Type species. *Terebratula humboldti* Hagenow 1842.

Diagnosis. Shell subquadrate to oval, costate. Brachial fold distinct. Well-defined pedicle sulcus bounded by faint carinae. Umbo slightly produced, beak suberect. Foramen small, circular, mesothyridid. Interarea extensive. Symphytium well exposed. Cardial process massive, bilobed. Hinge-plates thickened, fused. Median septum low. Anterior commissure intraplicate.

Ruegenella humboldti (Hagenow 1842)

Figs 11–13.

1842 *Terebratula Humboldti* Hagenow : 539 ; pl. 9, fig. 5a–c.
1850 *Terebratula Humboldti* Hagenow ; Geinitz : 210.
1856 *Terebratula Humboldti* Hagenow ; Boll : 210.
1871 *Terebratula Menardii* Quenstedt : pl. 44, fig. 69.
1909 *Terebratella Humboldti* Hagenow ; Nielsen : 168 ; pl. 2, figs 102–105.
1965 *Gemmarcula humboldtii* (Hagenow) Steinich : 160 ; pl. 19, fig. 1.
1972 *Gemmarcula humboldtii* (Hagenow) ; Surlyk : 24.

Description. *Ruegenella* with 35–40 strong rounded costae interrupted by transverse ornament of numerous fine lamellae and six or seven concentric growth-lines. The well-defined pedicle sulcus originates from the extreme posterior end of the umbo and widens anteriorly, remaining at a consistent depth ; it is bordered by faint carinae.

Internal characters. The transverse serial sections given here, Fig. 13, show the thickened shell, fused dental lamellae and very much reduced and thickened median septum supporting fused, poorly-defined hinge-plates. The disc-like cardinal process shows a more advanced development than that seen in *Gemmarcula*, having more acute indentations in the central part of the wall of the disc, making two almost complete tube-like extensions which are produced posteriorly (Fig. 12).

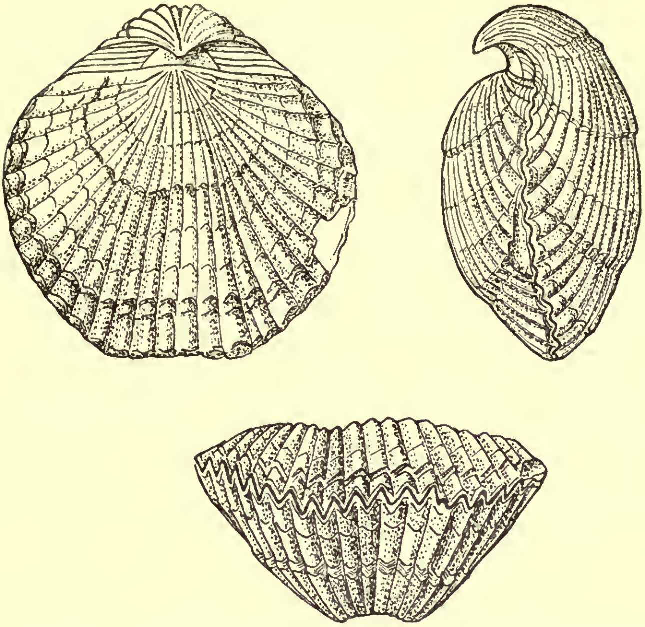


Fig. 11. *Ruegenella humboldti* (Hagenow) from the Maastrichtian of Rügen, north Germany. The general outline, costation and anterior folding are very similar to those of *Gemmarcula*. × 3.

The hinge-trough is shallow and not raised above the floor of the brachial valve. The descending branches of the brachial loop are given off directly from the distal ends of the hinge-trough without the development of any discernible crural bases as noted in *Gemmarcula*.

Remarks. In placing *T. humboldti* Hagenow in the genus *Gemmarcula*, Steinich (1965) was influenced very greatly by the similarity between the early ontogenetic stages which he had dissected from Chalk specimens and those of *Gemmarcula aurea*, the type species, which had been so carefully prepared and described by Elliott (1947). Steinich referred particularly to the lateral flanges on the transverse band of the mature loop and used this as a strong argument for assigning the species to *Gemmarcula*. This, with the surprisingly similar external morphological details, was sufficient evidence at that time. However, Elliott (1957 : 334–336) states that the flanges described on the transverse band of the type species are not now considered to be of diagnostic importance, as has already been pointed out with reference to *Gemmarcula* (p. 213).

Two other species are recognized as referable to *Ruegenella*. One is the large Maastrichtian species described as *Terebratella corneti* by Hanstein (1879) from Ciply, Belgium, represented here by a specimen from the Craie Phosphatée of Ciply (Pl. 1, figs 9a–c). It can be distinguished from *R. humboldti* by its considerably larger dimensions, massive truncated umbo, broad or extensive interarea and wider hinge-line.

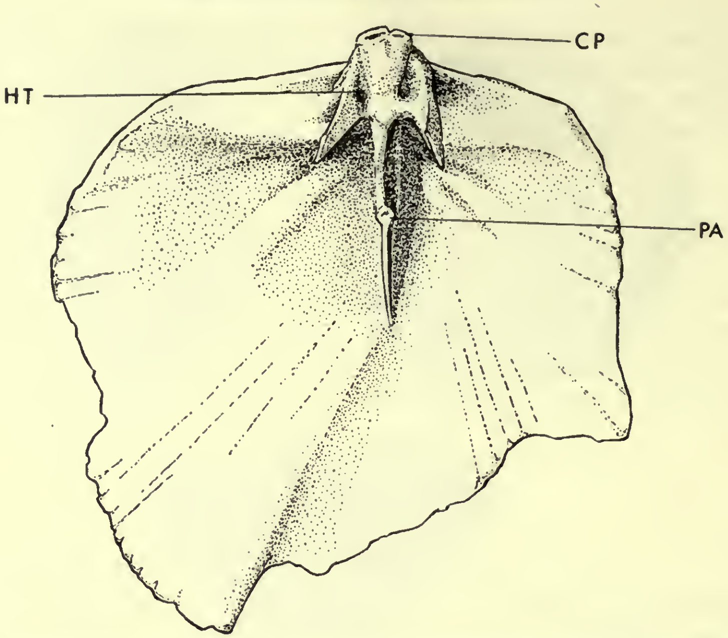


FIG. 12. Brachial valve of *Ruegenella humboldti* (Hagenow), showing the somewhat produced cardinal process CP with central depressions almost dividing it into two tubes. The hinge-trough HT is shorter and shallower than in *Gemmarcula* and the point of attachment for the brachial loop PA is placed more posteriorly on a proportionately shorter median septum. × 6.

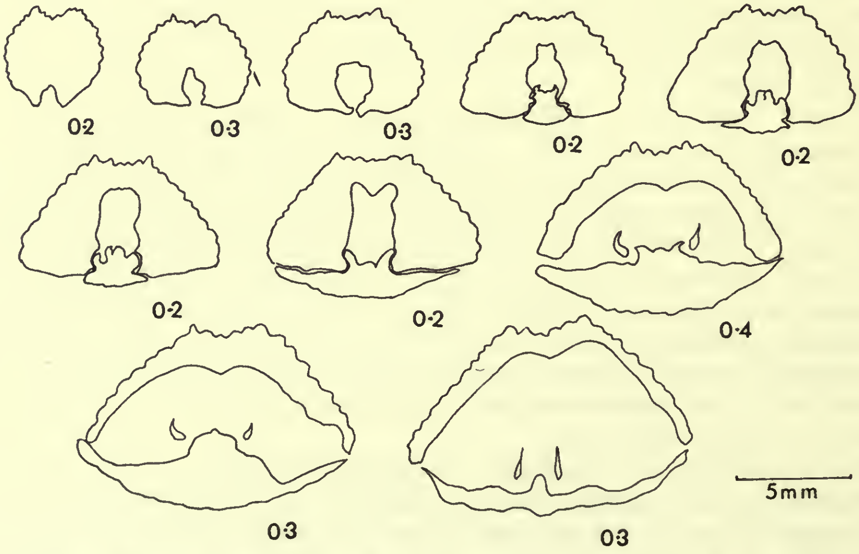


FIG. 13. Serial sections of *Ruegenella humboldti* (Hagenow), showing the grossly thickened pedicle umbo and fused dental lamellae, bifid cardinal process and massive, low median septum.

The other species, from the same locality and horizon, is described here briefly as *Ruegenella ciplyensis* sp. nov.

Ruegenella ciplyensis sp. nov.

Pl. 1, figs 5a–c.

Description. Small, subcircular *Ruegenella*, approximately 9 mm long, 10 mm wide and 6 mm in thickness. The umbo is massive and truncated by a comparatively large circular mesothyridid foramen. The shell ornament consists of 20–24 coarse radiating costae with well-marked transverse lamellar ornament on each valve. The interarea is flat and extensive and the break-ridges sharply defined. A broad low brachial fold develops anteriorly and there is a corresponding shallow sulcus in the pedicle valve. A fairly strong antiplicate anterior commissure is developed in the mature form.

Holotype. From the Craie Phosphatée of the Upper Chalk, Ciply, Belgium, in the Walker Collection, British Museum (Natural History), BB 45963. Dimensions: length 9·1 mm, width 9·9 mm, thickness 6·0 mm.

Paratypes. B 6655, B 15388, BB 45980–91. Also from the Craie Phosphatée, Ciply, Belgium, in the British Museum (Natural History).

Remarks. In general morphology this species resembles the associated *Ruegenella corneti* (Hanstein), but differs in being considerably smaller, and in the coarser radial ornament and more marked transverse lamellar ornament of the shell. The anterior commissure has a much more acute antiplication than *R. corneti* and in many ways resembles that of *Gemmarcula aurea* Elliott. *Ruegenella ciplyensis* differs from *R. humboldti* (Hagenow) in having a more massive umbo, coarser costae and wider hinge-line.

The species appears to be confined to the Craie Phosphatée of the Ciply district in much the same way as *R. corneti*.

Subfamily **UNCERTAIN**

Genus ***OBLONGARCULA*** Elliott 1959

Oblongarcula alemannica sp. nov.

Fig. 14; Pl. 3, figs 5a–c.

1836 *Terebratula oblonga* Sow.; Roemer : 46; pl. 2, fig. 23a–c.
1836 '*Terebratula reticulata* Schloth., var. *angusta* Sow.'; Pusch : 24; pl. 3, fig. 11a, b, c, d.
1839 *Terebratula pectiniformis* Roemer : 20; pl. 18, fig. 9 (non Schlotheim).
1840 *Terebratula puscheana* Roemer : 114; pl. 16, fig. 29.
1848 *Terebratella oblonga* d'Orbigny : 113; pl. 515, figs 7–19.
1850 *Terebratula oblonga* Sow.; Strombeck & von Buch : 76; pl. 4, figs 1–19.
1871 *Terebratula puscheana* Roemer; Quenstedt : 275; pl. 44, fig. 139.

Diagnosis. *Oblongarcula*, biconvex, elongate-oval to subpentagonal, costate to costellate. Umbo massive, beak suberect; beak-ridges distinct, mesothyridid. Anterior commissure rectimarginate through uniplicate to antiplicate. Disc-like cardinal process poorly developed. Fused hinge-plates supported by high, persistent median septum.

Description. Although typically oval in general outline with strong, deeply incised radiating costae, the species shows a considerable range of variation. The hinge-line in some variants extends laterally, increasing the flat interarea and exposing well-defined conjunct deltidial plates. This type of development is not a common variation but, when it occurs, produces a much flatter variety with young forms proportionately wider than long. Roemer (1839 : 20 ; pl. 18, fig. 9) described what he thought was one of these variants as *Terebratula pectiniformis hilseana*, but the separate name is not justified.

Another marked variant was originally described by Pusch (1836 : 24) as a variety of *Terebratula reticulata* Schlotheim and was subsequently redescribed as *Terebratula puscheana* by Roemer (1840 : 114 ; pl. 16, fig. 29). It is from the Hilsconglomerat, Berklingen, and differs from the typical *O. alemannica*, described here,

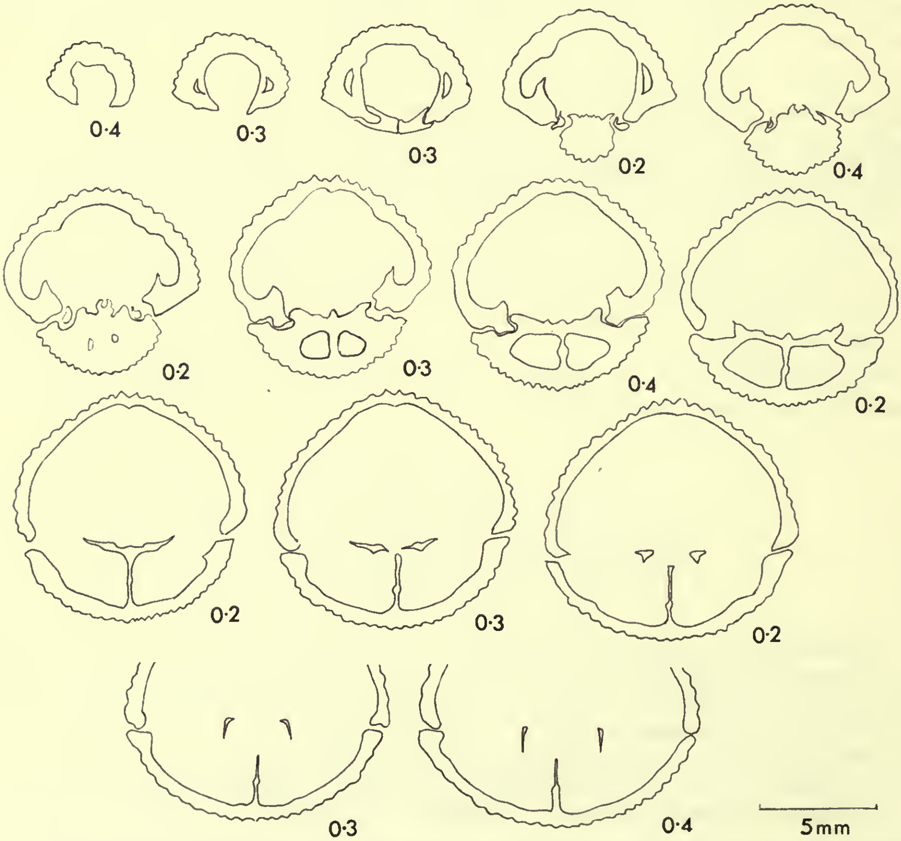


Fig. 14. Fourteen serial sections of a specimen of *Oblongarcula alemannica* sp. nov. showing the strong persistent brachial septum and elongate-triangular hinge-plates, as seen in the type species *Oblongarcula oblonga*.

in having finer radial shell ornament consisting of numerous intercalating and bifurcating costellae interrupted by well-marked concentric growth-lines. The anterior commissure of this variety is often strongly antiplicate and this feature alone might have provided sufficient reason for the two variants having been separated. There is ample evidence of human sorting in most of the collections examined.

Strombeck & von Buch (1850) figured a very convincing series of specimens (pl. 4) showing gradation from the typical oval, strongly costate form, to the almost smooth antiplicate varieties together with numerous costate and semicostate intermediate forms. All the specimens are from the Hauterivian of the Hanover–Brunswick district of north Germany. A similar series of eleven variants exists in the Davidson Collection (BM(NH) B 1200) from the Neocomian of Schoppenstedt, Germany. Specimens exhibiting intermediate characters also occur in the Lower Cretaceous, Hauterivian, of the Haute Marne, France and several examples of these are also in the Davidson Collection (BM(NH) B 6678 and B 6690).

HOLOTYPE. *Oblongarcula alemannica* sp. nov. was originally described by Roemer (1836 : 46), as *Terebratula oblonga* Sow., from the Hilsthon of the Hilsconglomerat, Elligser Brinke, near Hanover, north Germany. These beds are considered to be of Hauterivian age by present German workers. Roemer was obviously under the impression that his species was synonymous with the species previously described by J. de C. Sowerby (1829) from the Aptian of England. It would have been appropriate to choose Roemer's specimen as the holotype of *O. alemannica* but the original was lost during World War II. As holotype for *Oblonga alemannica* sp. nov., a specimen closely resembling Roemer's original is here selected from a series of five in the Hildesheim Museum, from the Hilsconglomerat of Berklingen. It has been registered as RM 756.

REMARKS. The extremes of variation noted within this species are admittedly broad and such differences may be of minor stratigraphical significance. But this has still to be demonstrated and, for the time being, it would be preferable not to use more than one taxon.

O. alemannica is not uncommon in the argillaceous beds of Hauterivian age at Grenslerberg, Schoppenstedt, Berklingen and Gros Vahlberg in north Germany and also from beds of similar age and lithology at St Dizier, Haute Marne, France. Records of its occurrence in Spain and southern France have not been substantiated.

Although it is not suggested there is any direct relationship, it is interesting that a somewhat similar range of variation occurs in the Middle Liassic species *Fimbriothyris guerangeri* (Eudes-Deslongchamps) which also has an arrangement of cardinalia and brachial loop like that of *O. alemannica* (Muir-Wood 1965 : H828). Eudes-Deslongchamps (1862–85 : 23 ; pl. 23, figs 4–10) figures a series of specimens showing a full range of morphological variation, from strongly costate to polyplicate with an almost smooth shell surface, a range which is in many ways similar to that of the species described here.

DIMENSIONS. Holotype, 18·9 mm long, 14·7 mm wide and 12·5 mm thick. Other specimens, all in the British Museum (Natural History), London, have dimensions as follows (measurements in mm).

	Length	Width	Thickness
(a), from the Haute Marne, France			
B 6678	21·5	16·1	11·0
	17·8	13·3	9·9
(b), from Schoppenstedt, north Germany			
B 12000	18·1	13·0	12·1
	16·9	11·5	10·0
	16·0	11·9	10·0
	15·9	12·1	9·4
(c), from Berklingen, near Brunswick, north Germany			
B 21920	16·8	12·1	9·9
	17·8	12·9	10·4
	15·9	10·7	7·6

Oblongarcula oblonga (J. de C. Sowerby 1829)

Figs 15–16 ; Pl. 2, figs 10a–c ; Pl. 3, figs 1a–c.

1829 *Terebratula oblonga* J. de C. Sowerby : 68 ; pl. 535, figs 4, 5, 6.
1838 *Terebratula oblonga* Sow. ; von Buch : 159 ; pl. 16, fig. 2.
1845 *Terebratula oblonga* Sow. ; Forbes : 346.
1852 *Terebratella fittoni* Meyer ; Davidson : pl. 8, figs 8–13 [non Meyer].
1864 *Terebratula oblonga* Sow. ; Meyer : 254 ; pl. 11, figs 12–14.
1874 *Terebratella oblonga* (Sow.) Davidson : 26 ; pl. 2, figs 29–31.
1959 *Oblongarcula oblonga* (J. de C. Sowerby) Elliott : 147.

EMENDED DESCRIPTION. Elongate-oval, acutely biconvex *Oblongarcula*, with numerous radiating, sharply angular costae, often deeply incised and with occasional bifurcation. Rectimarginate to incipiently uniplicate, with almost imperceptible median fold on brachial valve. Massive umbo truncated by large circular

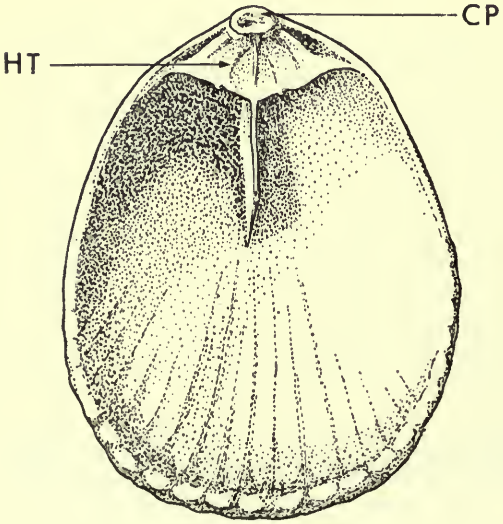
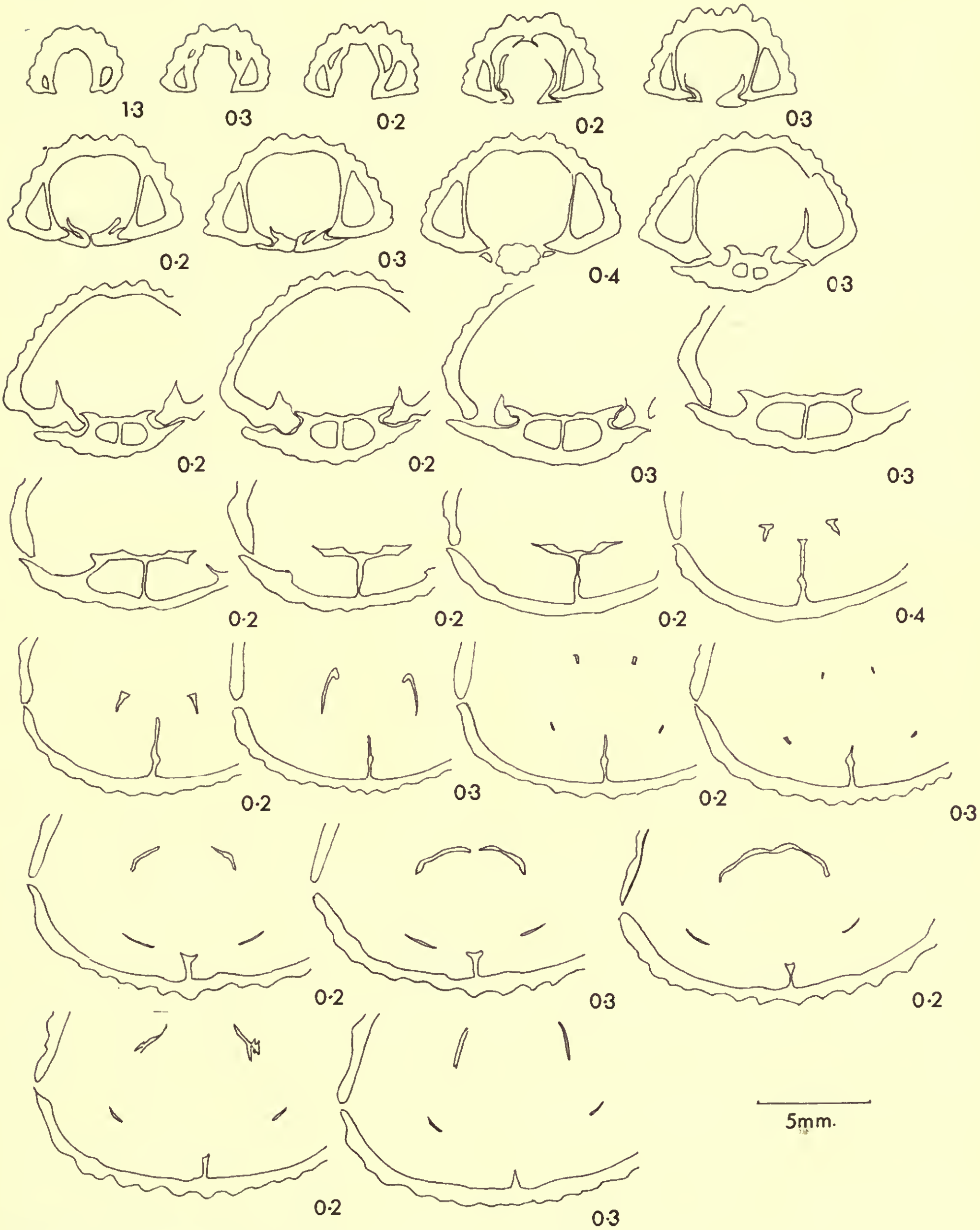


FIG. 15. Brachial valve of *Oblongarcula oblonga* (J. de C. Sowerby) from the Upper Aptian, Faringdon, Berkshire, showing the typical disc-like cardinal process CP and the broad, comparatively shallow hinge-trough HT. ×4.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0·2
0·3
0·3
0·2
0·2
0·2
0·4
0·2
0·3
0·2
0·3
0·2
0·3
0·2
0·2
0·3
5mm.

FIG. 16. Transverse serial sections through a specimen of *Oblongarcula oblonga* (J. de C. Sowerby) from the Upper Aptian, Hythe Beds, Hythe, Kent, showing the well-developed pedicle collar in the pedicle umbo and the broad, shallow hinge-trough, long triangular hinge-plates and high persistent supporting median septum in the brachial valve.

foramen. Conjunct deltidial plates well exposed. Extensive triangular interarea bordered by sharp or well-defined beak-ridges.

Internal structure shows well-defined pedicle collar situated between early-developing, slightly divergent, sub-parallel dental lamellae enclosed within callus at posterior end of pedicle valve. As seen in successive serial sections, the transversely elliptical, disc-like cardinal process develops early from the posterior extremity of the brachial umbo. A wide rectangular hinge-trough develops and extends anteriorly, becoming shallower and maintaining a broad shallow depression. The distal ends of the hinge-trough give rise to elongate-triangular hinge-plates supported by a high, persistent median septum. Massive, subquadrate hinge-teeth are deeply inserted with extensive inner and outer socket-ridges. No attachment of brachial loop to median septum noted in serial sections.

HOLOTYPE. B 61628 in the Sowerby Collection, British Museum (Natural History), London, from the Upper Aptian Sponge Gravel, Faringdon, Berkshire.

DIMENSIONS. Holotype, 21·9 mm long, 16·5 mm wide and 13·6 mm thick. Other specimens from the same formation, all in the British Museum (Natural History), have dimensions as follows (measurements in mm).

	Length	Width	Thickness
B 25979	21·2	17·3	14
	22·4	17·1	13
	23·0	18·0	12·5
	22·6	19·0	13·7
	20·0	15·1	12·8
BB 3542	20·2	15·7	12·4
BB 3543	18·4	14·5	11·1
BB 3544	15·8	11·9	9·9

DISTRIBUTION. Apart from its occurrence in the Upper Aptian Lower Greensand, at Faringdon, Berkshire, *O. oblonga* also occurs at a similar horizon in the ferruginous deposits at Seend, Wiltshire, in the Hythe Beds of the Folkestone and Maidstone districts of Kent and in the Lower Greensand, *Parahoplites nutfieldensis* Zone, at Atherfield and Shanklin, Isle of Wight. A well-marked variant occurs in the Bargate Beds at Guildford and Godalming, Surrey and in the Upper Aptian beds of Brickhill, Bedfordshire and Upware, Cambridgeshire. It differs from the typical form in its smaller size, more regular oval outline, finer and less incised costae and more obvious growth-lines.

REMARKS. The relationship between *O. oblonga* and the foregoing *Oblongarcula alemannica* sp. nov., from the Hauterivian of north Germany and France, appears to be a direct one. The external morphology of the two forms is very similar and this was why Roemer (1836) assigned his specimen from the Hilsthon of Elligser Brinke to Sowerby's *Terebratula oblonga.* There are, however, certain minor differences in internal structure which should be noted. In successive sections a small amorphous calcareous structure is seen to precede the development of the hinge-plates in *O. alemannica* and occupy a vague position approximately in the centre

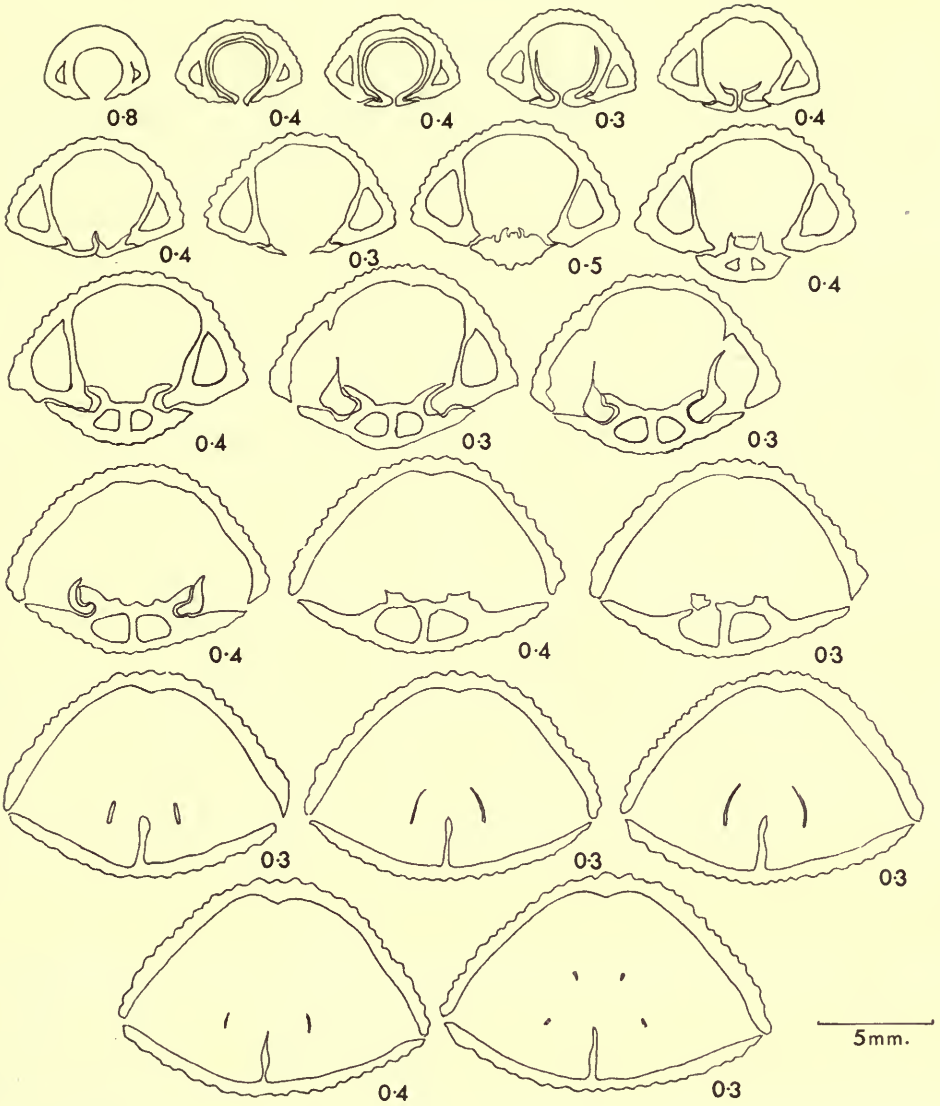

FIG. 17. *Oblongarcula davidsoni* (Walker) from the Upper Aptian of Upware, Cambridge. A series of serial sections justifying its assignment to *Oblongarcula*.

of the hinge-trough. It does not persist and soon flattens as the hinge-plates develop anteriorly.

It is probable that the species described by Walker (1867) as *Terebratella davidsoni*, from the Lower Greensand of Upware, is a further development or lateral variation of the main *oblonga* stock ; it is assigned here to the genus *Oblongarcula* (Fig. 17 ; Pl. 3, figs 7a–c).

Genus *ARENACIARCULA* Elliott 1959

TYPE SPECIES. *Terebratella fittoni* Meyer 1864.

EMENDED DESCRIPTION. The original description given by Elliott (1959 : 147) was brief and did not mention any transverse serial sections of the type species. The emendation given here includes serial sections, Fig. 18, below, for comparison with those of *Oblongarcula oblonga* J. de C. Sowerby, Fig. 16, p. 231, and *Gemmarcula aurea* Elliott, Fig. 2, p. 212.

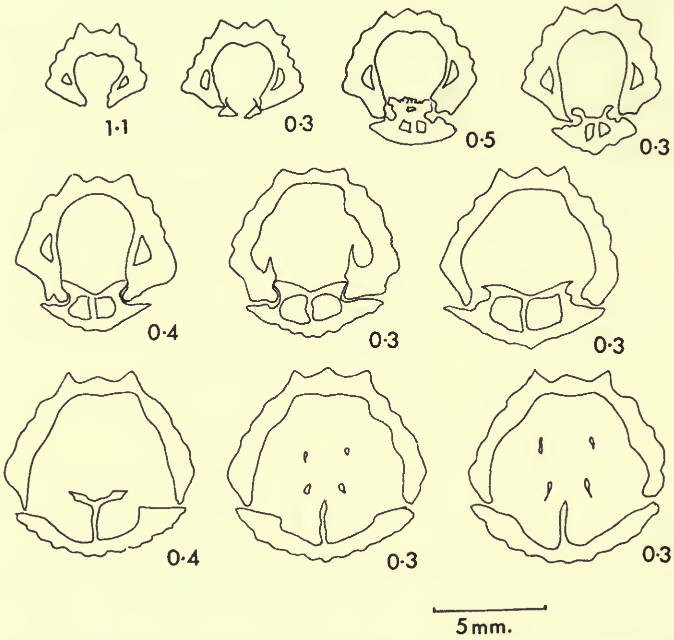

FIG. 18. A series of ten serial sections through a specimen of *Arenaciarcula fittoni* (Meyer) from the Upper Aptian of Brickhill, Buckinghamshire.

The sections show that the test of *Arenaciarcula* is thicker than in either *Gemmarcula* or *Oblongarcula* and that the cardinal process is more highly developed. The dental lamellae appear to be stronger or more persistent in *Arenaciarcula* and the median septum, which supports the hinge-plates in the same way as is seen in *Oblongarcula*, breaks away much more quickly, leaving thick, comparatively shorter, triangular hinge-plates to form the crural bases and to develop long crural processes ventrally. The septum persists anteriorly for over two-thirds of the length of the valve and must have formed a firm point of attachment for the brachial loop in earlier developmental stages. No attachment of brachial loop to septum appears in any of the serial sections so far examined.

RANGE. Upper Aptian to Middle Cenomanian.

Arenaciarcula fittoni (Meyer 1864)

Figs 18, 19; Pl. 2, figs 8a–c.

1836 *Terebratula quadrata* J. de C. Sowerby in Fitton : pl. 16, fig. 9.
1864 *Terebratella fittoni* Meyer : 250 ; pl. 11, figs 1–10.
1872 *Terebratula* (*Terebratella*) *fittoni* Meyer ; Pictet : 129 ; pl. 207, fig. 2a–c.
1874 *Terebratella fittoni* Meyer ; Davidson : 26 ; pl. 8, figs 8–13.

DESCRIPTION. Although adequately described by Meyer (1864), a certain amount of confusion has arisen between this species and *Oblongarcula oblonga* (J. de C. Sowerby). To a certain extent this is understandable, since the two forms have much in common. They are both comparatively small oval species with sharp, suberect beaks, well-marked beak-ridges and strong radiating costae. A more critical examination of both forms reveals that *A. fittoni* is more uniform in size and outline. It has a fairly well-marked, but not highly developed, median fold in the brachial valve and sometimes a faint corresponding sulcus in the pedicle valve. It is also narrower and more acutely biconvex than *Oblongarcula oblonga*.

Meyer stated in the original description (1864 : 250) that the species could be 'distinguished from *T. oblonga* by its diminutive size and by the smaller number and inequality of the ribs.' It also has a more highly developed cardinal process and a shorter, more acutely triangular and deeper hinge-trough.

TYPE SPECIMEN. Some of Meyer's material can be found among the Davidson Collection in the British Museum (Natural History), but no specimens which might have been designated type or which Meyer might have used in the original description of *T. fittoni* have been found. It is still possible that his original specimen may be found among the collections of the Sedgwick Museum, Cambridge or in the general collections of the BM(NH), and so the question of designating a neotype for the species should remain for the time being.

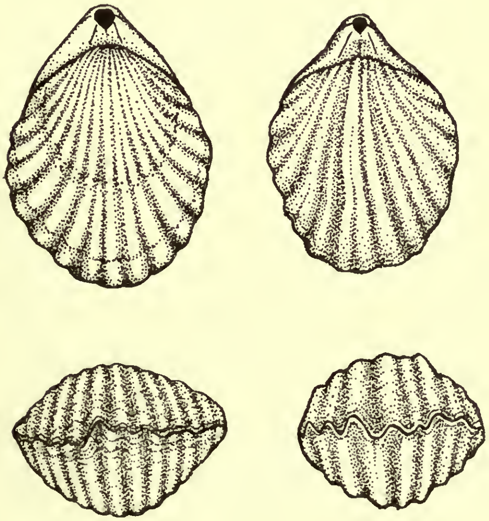

FIG. 19. Diagram of two specimens of *Arenaciarcula fittoni* (Meyer) from the Upper Aptian of Brickhill, Buckinghamshire, showing variation in general outline, beak characters, costae and anterior commissure. × 3.

DISTRIBUTION. *Arenaciarcula fittoni* appears to be confined to beds within the Upper Aptian and is found in the Lower Greensand at Upware, Cambridge and at the same horizon at Brickhill, Buckinghamshire. It also occurs in the Bargate Pebble Bed at Tewsley, Guildford, and Godalming, Surrey, from where it was originally described by Meyer, and also from the Upper Aptian at Maidstone and Sevenoaks, Kent. A specimen figured by Pictet (1872 : pl. 207, fig. 2a–c) was accompanied by a brief description but no locality was given. From its appearance it almost certainly originated from England and was probably presented to Pictet by Meyer.

REMARKS. Confusion with *O. oblonga* may have created a wrong impression regarding its occurrence. The species is, in fact, comparatively rare. Although often found in association with *O. oblonga*, it seems to have been more rigidly controlled by ecological conditions.

Arenaciarcula beaumonti (d'Archiac 1847)

Fig. 20 ; Pl. 2, figs. 7a–c.

1847 *Terebratula Beaumonti* d'Archiac : 331 ; pl. 21, figs 12–14.
1852 *Terebratula oblonga* Sow. ; Davidson : 51 ; pl. 2, figs 32, 32a–b.
1867 *Terebratula* (?) *Beaumonti* d'Archiac ; Schloenbach : 461 ; pl. 22, figs 3–5.
1869 *Trigonosemus kiprijanovi* Hofman : 25 ; pl. 5, figs 18–21.
1871 *Terebratula orbicularis* Sow., Quenstedt : 293 ; pl. 45, figs 63–69.
1874 *Terebratella Beaumonti* (d'Archiac) Zareczny : 177 ; pl. 2, fig. 2.
1916 *Terebratella Beaumonti* (d'Archiac) ; Ravn : 22 ; pl. 4, fig. 8.
1969 *Terebratella beaumonti* (d'Archiac) ; Panow : 593 ; pl. 112, fig. 5.
1972 *Oblongarcula beaumonti* (d'Archiac) Popiel-Barczyk : 127 ; pl. 1, figs 1–5 ; pl. 4, fig. 3.

DESCRIPTION. D'Archiac's species has been recently reviewed and described by Popiel-Barczyk (1972 : 127), who gave a series of serial sections (: 130–133) and reconstructed the brachial loop of a specimen from the Cenomanian of Annopol, Poland. The transverse serial sections of *Arenaciarcula acuticostata* sp. nov., Fig. 21, p. 239, can be compared with these. At present nothing need be added to her definitive account.

Both series of sections show the typical bifid cardinal process with additional thickened myophore extension. This structure occupies an area just inside the pedicle umbonal cavity and in successive sections remains fairly well defined, with the development of steep-sided inner and outer socket-ridges. The hinge-trough is, therefore, deep and subquadrate in transverse outline. The hinge-plates are elongate-triangular and remain supported by the septum from the floor of the brachial valve for a comparatively short distance. This distinguishes it from the true *Oblongarcula* where the median septum supports the fused hinge-plates for a greater distance into the valve.

MATERIAL. Eleven specimens from English and European localities have been measured and are listed below. In addition there are two poorly-preserved internal moulds (B 40411) from Galicia, Austria, which are recognizable as typical forms.

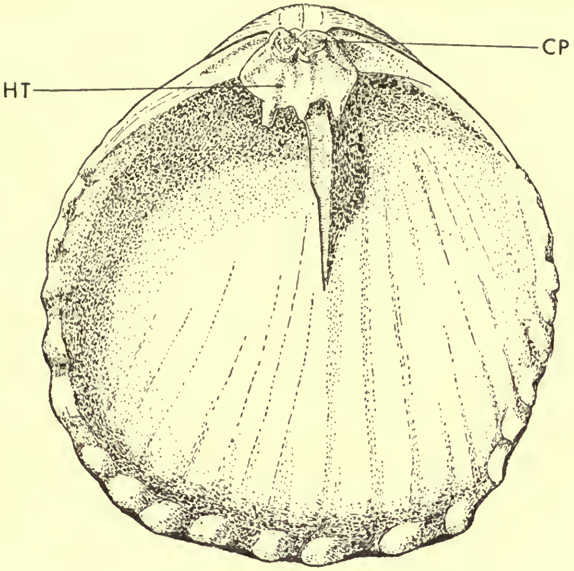

FIG. 20. Brachial valve of a specimen of *Arenaciarcula beaumonti* (d'Archiac) from the Tourtia of Tournai, Belgium, showing the comparatively well-developed bifid cardinal process CP and hinge-trough narrower than in *Oblongarcula*. × 4.

All the specimens are in the general collections of the British Museum (Natural History) (measurements in mm).

	Length	Width	Thickness
(a), from the middle Cenomanian Limestone, Wilmington, Devon			
BB 45977	10·7	9·0	7·6
BB 45978	9·2	8·0	6·2
BB 45979	10·0	8·0	7·0
(b), from the Tourtia of Tournai, Belgium			
B 35502	11·9	9·0	8·0
	11·0	8·9	7·9
	10·0	8·1	7·1
	10·0	9·0	6·2
	11·1	10·0	7·4
	10·0	8·0	6·0
	8·7	8·0	6·0
(c), from Essen, north Germany			
B 35684	9·9	7·9	6·0

REMARKS. In removing this species from the genus *Oblongarcula* into which it had somewhat tentatively been placed by Popiel-Barczyk (1972), I have no doubts that it should be classified with *Arenaciarcula fittoni* and *A. acuticostata* sp. nov., although no reconstructions of the loop structures have been prepared from serial sections.

Schloenbach (1867 : pl. 22, fig. 3e) shows a brachial valve of a specimen with exposed loop having a point of attachment to the septum at approximately mid-point of the valve. His fig. 5 shows a slightly reconstructed valve and loop with attachment bands of loop to septum and elongated lateral spurs or 'flanges' on the transverse band of the loop. These illustrations confirm the descriptions and reconstructions, showing similar lateral spurs, given by Popiel-Barczyk (1972 : 131).

The species is more widespread geographically than some of its associated fauna and occurs, as stated, in the Tourtia of Belgium, the same horizon in the Essen Greensand of north Germany, the Cenomanian of Annopol, Poland and Russia, in the basal conglomerate on Bornholm, Denmark and in the Cenomanian Limestone of Wilmington, Devon. A similar species, although not regarded here as conspecific, was described by Vantschurov (1966 : 110 ; figs 3, 4) from the Cenomanian of Turkmenistan as *Trigonosemus kamyschalaensis*. From the associated transverse serial sections, the species is clearly congeneric with *A. beaumonti* and is referred here to *Arenaciarcula*.

Although bearing a superficial resemblance to *Oblongarcula oblonga*, *Arenaciarcula beaumonti* can be distinguished by its more acutely biconvex outline, deeply incised radiating costae very rarely bifurcating, its narrower hinge-line and constant rectimarginate anterior commissure. The internal structures differ in their cardinalia and loop morphology.

Arenaciarcula acuticostata sp. nov.

Fig. 21 ; Pl. 2, figs 6a–c.

1903 *Terebratella hercynica* (Schloenbach) Walker : 257 ; pl. 18, fig. 4a–c (non Schloenbach).

DIAGNOSIS. Acutely biconvex *Arenaciarcula*, triangular in general outline. Average length 17 mm, width 14 mm and thickness 13 mm. Costae sharp, deeply incised. Umbo slightly produced, beak suberect. Beak-ridges sharp ; interarea short. Anterior commissure rectimarginate.

DESCRIPTION. This species was originally described by Walker (1903 : 257) as *Terebratella hercynica* (Schloenbach), from the Lower Albian of Leighton Buzzard, Bedfordshire. Walker confused his specimen with the species described and figured by Schloenbach (1867 : 467 ; pl. 22, figs 6, 7) from the Cenomanian of Laugenberges near Quedlinburg, north Germany. The two species are, however, quite distinct and are assigned to different genera on the grounds of their internal structures.

The serial sections of *A. acuticostata* given here (Fig. 21) have been compared with those made from duplicate specimens of *Arenaciarcula beaumonti* (d'Archiac) from the Tourtia of Tournai, Belgium, and may also be compared with a similar series presented by Popiel-Barczyk (1972 : 130) for a specimen of *A. beaumonti* (d'Archiac) (under the name of *Oblongarcula beaumonti*) from the Cenomanian of Annopol, Poland. It will be seen that the two forms have generally similar cardinal processes and cardinalia, with the same or similar arrangement of hinge teeth and hinge-plate extensions. It will also be seen that the two species have similar triangular hinge-plates which, although initially fused, are not supported for a great distance by the median septum of the brachial valve and soon break away with the development of the crural bases and descending branches of the loop. The branches themselves remain fairly close to the septum, a character noted in serial sections of *Terebrirostra* and *Dereta*.

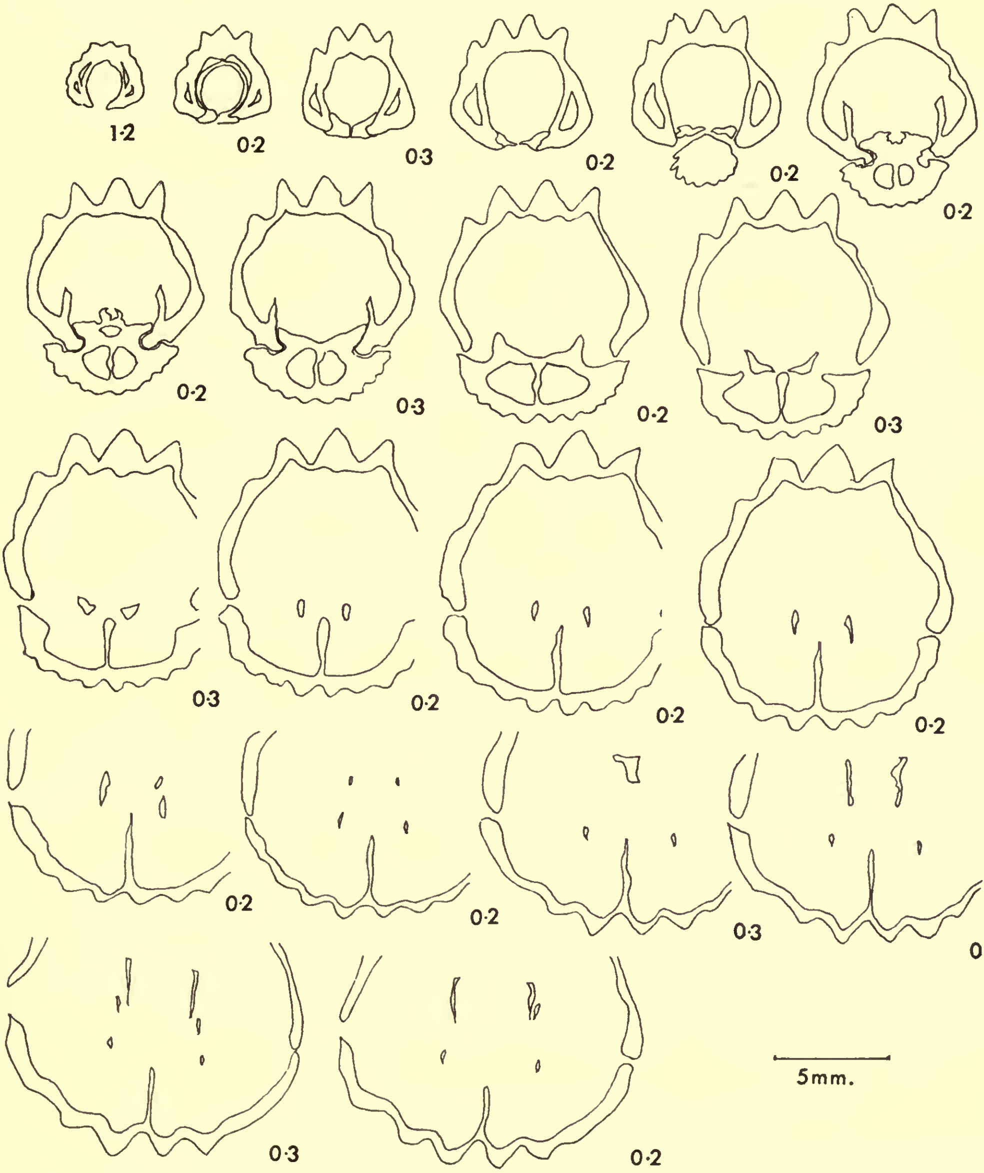

Fig. 21. *Arenaciarcula acuticostata* sp. nov. from the Lower Albian, Leighton Buzzard, Bedfordshire. A series of serial sections which can be compared to those of *A. beaumonti* (d'Archiac) from the Cenomanian of Annopol figured by Popiel-Barczyk (1972).

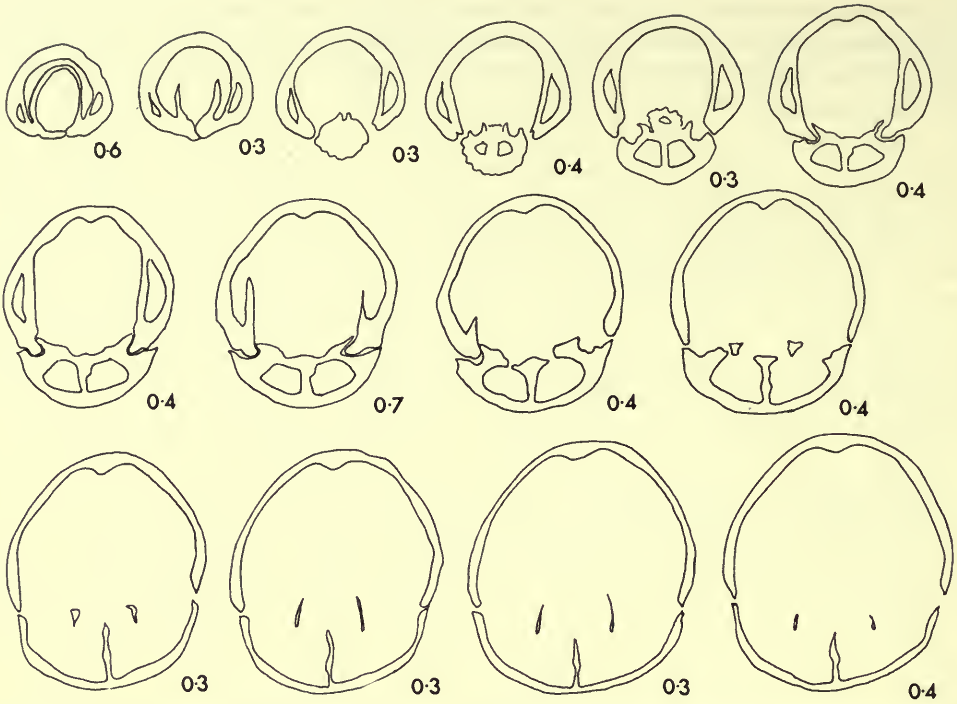

Fig. 22. Transverse serial sections of a specimen of '*Terebratella*' *keepingi* Walker from the Upper Aptian of Brickhill, Buckinghamshire. The species is somewhat tentatively assigned to *Arenaciarcula*. (See Pl. 3, fig. 3).

Holotype. The specimen described and figured by Walker (1903 : 257 ; pl. 18, fig. 4a–c) as *Terebratella hercynica* (Schloen.) and now in the collections of the Institute of Geological Sciences, London, registered as GSM 51275, is chosen as holotype of *Arenaciarcula acuticostata* sp. nov. Dimensions : length 16·6 mm, width 14·2 mm and thickness 13·0 mm.

Remarks. The species appears to be confined to the Lower Albian of Shenley Hill and other localities in the Leighton Buzzard district. Smirnova (1972 : pl. 9, fig. 2), however, figured a specimen from the Upper Albian of the Tekedzhik, Turkmenistan SSR, as *Eudesia tekedgikensis* ; it bears a very strong resemblance to *Arenaciarcula acuticostata* sp. nov., but no serial sections were given.

Family **TEREBRATELLIDAE** King 1850
Subfamily **TRIGONOSEMINAE** Elliott 1965
Genus ***TRIGONOSEMUS*** Koenig 1825

Type species. *Trigonosemus elegans* Koenig 1825.

Trigonosemus elegans Koenig 1825

Figs 23, 24 ; Pl. 3, figs 2a–c.

1825 *Trigonosemus elegans* Koenig : 3 ; pl. 4, figs 73a–e.
1848 *Fissurirostra elegans* d'Orbigny : 134 ; pl. 520, figs 9–13.
1848 *Fissurirostra pectita* d'Orbigny : 136 ; pl. 520, figs 14–18.
1848 *Fissurirostra recurva* d'Orbigny : 133 ; pl. 520, figs 1–8.
1852 *Trigonosemus elegans* Koenig ; Davidson : 29 ; pl. 4, fig. 3.

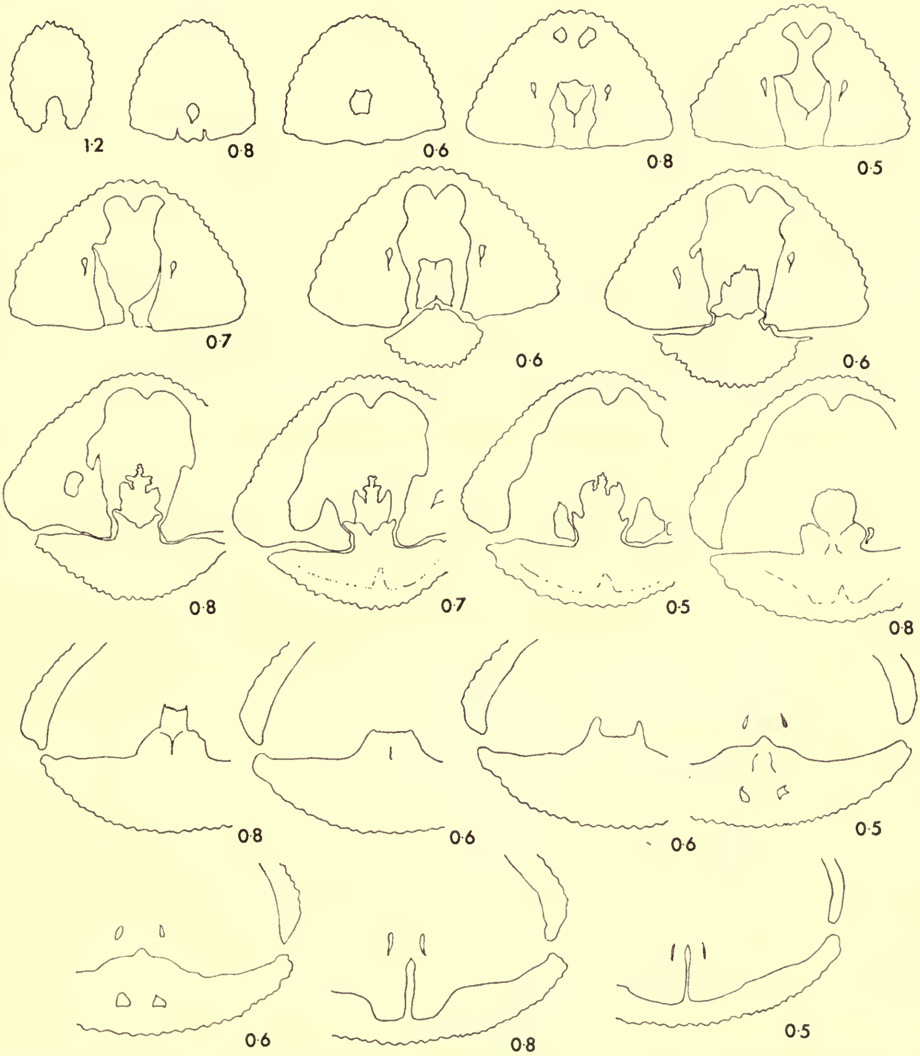

FIG. 23. A series of 19 serial sections through a specimen of *Trigonosemus elegans* Koenig from the Upper Chalk of Ciply, Belgium. This shows the extraordinary shell thickening and highly developed trifid cardinal process and semisphaeroidal cardinal bulge occupying the shallow hinge-trough.

EMENDED DESCRIPTION. *Trigonosemus*, elongate-oval to broadly pentangulate, averaging 22 mm in length, 21 mm in width and 17 mm in thickness. The pedicle umbo is broad and produced with a slightly incurved, acutely pointed beak. The beak-ridges are sharply defined and border a wide, extensive interarea. The permesothyridid foramen is small and circular in outline. Well-developed, faintly striate symphytium with conjunct deltidial plates. Anterior commissure sulcocarinate to elliptical in transverse outline. The shell surface is ornamented with approximately 50–55 rounded costellae with a tendency to bifurcation.

Internal structure. *T. elegans* is typified by a highly developed cardinal process, just anterior to the base of the trifid lobes of which is a semisphaeroidal bulge, similar in many respects to the thickened base of the cardinal process seen in *Pachymagas* and *Neothyris* from the Tertiary. This bulge usually occupies most of the area of the hinge-trough and is fused anteriorly with the hinge-plates. Other species within the genus, such as *T. pectiniformis* von Buch (Fig. 25 ; Pl. 1, figs 7a–c) and *T. palissyi* Woodward (Fig. 26), do not appear to have such advanced development of this character, although they have many of the other generic features.

In a description of *Trigonosemus pulchellus* Nilsson, Steinich (1965:176) illustrates altogether different cardinalia. His specimen is shown to have a produced posterior rim or ridge to the hinge-trough, with a centrally-developed low cardinal process which is divided longitudinally by a short, poorly-defined septum. This type of

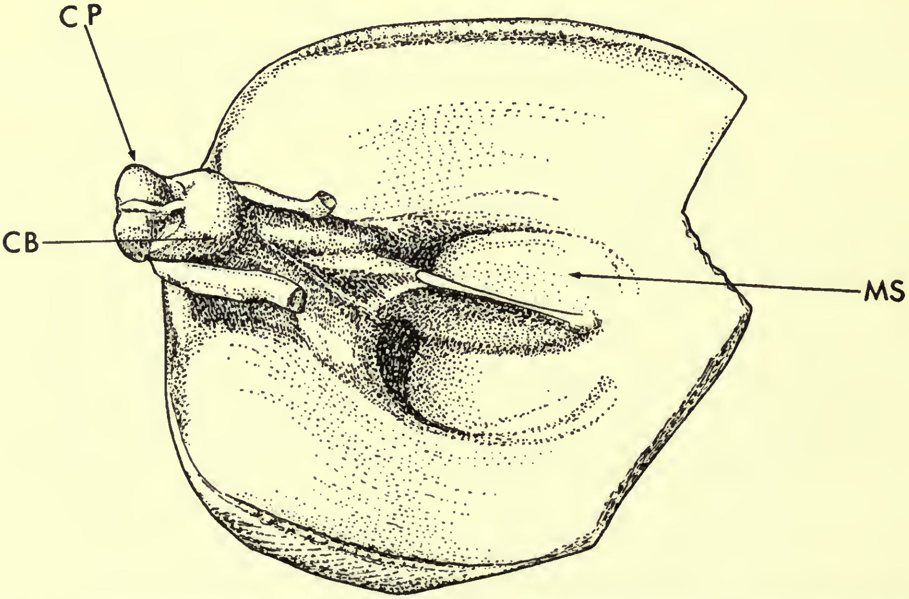

FIG. 24. The produced and highly developed trifid cardinal process CP and semisphaeroidal cardinal bulge CB are characters which distinguish *Trigonosemus elegans* Koenig from any other terebratellacean within the Cretaceous. The deeply sunken muscle-scars MS are also distinctive but not necessarily of generic importance. ×4.

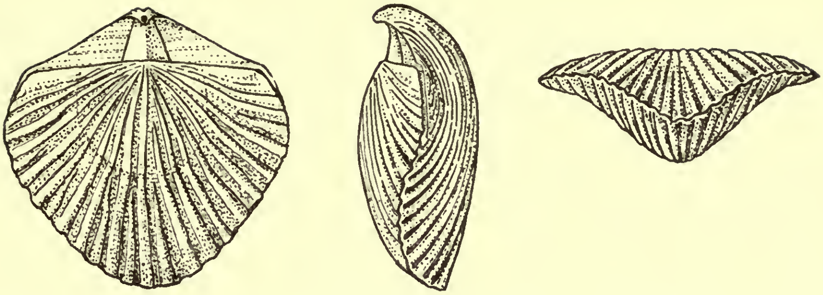

FIG. 25. Although assigned to the genus *Trigonosemus*, *T. pectiniformis* (von Buch) shows few of the external generic characters. It has differently shaped costae, which show fairly frequent intercalation, and has a well-marked anterior sulcus in the brachial valve. ×3.

cardinalia is so atypical of the genus *Trigonosemus* as to suggest that further investigation of the types and topotype material is needed. It may be found that *T. pulchellus* represents an undescribed line of development closely related to *Trigonosemus*.

The brachial loop of *T. elegans* is rarely preserved intact, but sufficient information has been obtained from broken loops to be reasonably certain that it is of a terebratellid development.

LECTOTYPE. Koenig did not indicate or designate any type material and the exact locality of his illustrated specimens (1825 : pl. 4, figs 73d, e) is not known. Within the general collections of the British Museum (Natural History) are two specimens from the S. P. Woodward Collection collected from the *Baculites* Zone

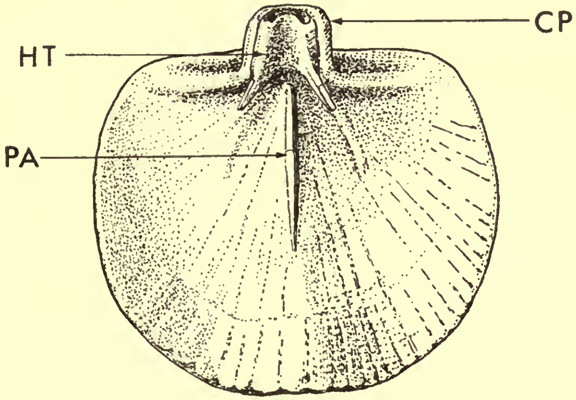

FIG. 26. *Trigonosemus palissi* (Woodward), from the Ciply Chalk, also departs from the typical form in having a completely different type of cardinal process, CP, which is shown as an elongation or posterior extension of the rim of the hinge-trough HT. The point of attachment of the brachial loop is approximately in the same position as in *Ruegenella* gen. nov. ×4.

of the Maastrichtian, near Caen, France. They comprise a brachial and a pedicle valve which resemble those figured by Koenig. Furthermore, Koenig was employed as curator of the fossil collections at the British Museum at the time the specimens were described and figured. G. R. Waterhouse has left an authoritative testament, recorded on the label of the subsequently curated valves, indicating that these were in fact the specimens figured by Koenig. One of these, the brachial valve, fig. 73d, is registered as B 81568, and is here selected as lectotype of the species *Trigonosemus elegans* Koenig 1825. Dimensions : length 17·9 mm, width 20·0 mm.

Remarks. *Trigonosemus elegans* is a comparatively rare fossil occurring in the Upper Chalk, Maastrichtian, Ciply, Belgium and at the same horizon in Holland, as well as at the type locality near Caen, Normandy, France.

In Britain, specimens assigned to *Trigonosemus elegans* have been found in the Upper Senonian of Norwich, Norfolk and in Chalk detritus at Charing, Kent. The Kentish specimen, figured by Davidson (1852 : pl. 4, fig. 3), is flatter and considerably smaller than the typical form and, although obviously congeneric, may not belong to the type species *T. elegans*.

Dimensions. Other specimens from the Maastrichtian of Ciply, Belgium, all in the British Museum (Natural History), have dimensions as follows (measurements in mm).

	Length	Width	Thickness
BB 45974 (Pl. 3, figs 2a–c)	27·1	23·1	16·0
B 35508	28·0	21·5	18·2
	28·0	23·6	17·0
	25·0	21·4	14·8
	27·0	23·0	16·2
B 46338	23·1	21·6	12·2
B 46340	24·0	21·6	14·5
B 46341	26·3	25·0	15·2
	16·8	15·0	8·2

Genus *TEREBRIROSTRA* d'Orbigny 1850

Type species. *Terebratula lyra* J. Sowerby 1816.

Terebrirostra arduenensis d'Orbigny 1850

1850 *Terebrirostra arduenensis* d'Orbigny : 128 ; pl. 519, figs 60, 61.
1872 *Terebratula (Terebrirostra) arduenensis* d'Orbigny ; Pictet : 132 ; pl. 207, fig. 13.
1903 *Terebrirostra lyra* (Sow.) var. *incurvirostrum* Walker : 255 ; pl. 18, figs 1a–b, 2a–b.
1934 *Terebrirostra incurvirostrum* Lamplugh & Walker ; Muir-Wood : 554 ; fig. 14.

Description. The original description by d'Orbigny (1850 : 128) and the additional description given by Pictet (1872 : 132) are adequate for the species, but the internal structure of the genus was not fully understood until Muir-Wood (1934 : 553) figured a series of transverse serial sections through the umbo of a specimen of the type species *T. lyra* (J. Sowerby) from the Cenomanian of Warminster, Wiltshire.

She used this information to compare with the internal structures seen in a series of longitudinal sections (1934 : fig. 14) through a specimen of *Terebrirostra incurvirostrum* Walker from the Lower Albian of Shenley Hill, Leighton Buzzard, Bedfordshire. Muir-Wood's serial sections illustrate the extraordinary length of the dental lamellae which originate from the extreme posterior end of the produced pedicle umbo and show the trifid cardinal process and extended hinge-plates protruding into the pedicle umbonal cavity.

The hinge-plates develop directly from a short, shallow hinge-trough, their distal ends giving rise to the descending branches of the brachial loop which remain close to the median septum, broadening anteriorly. The general arrangement of the cardinalia and shape of the hinge-plates is very similar, although not identical, to those of *Dereta* (Fig. 29, p. 248). It is probable that both genera have been developed from the same original stock, possibly related to a late Jurassic or early Cretaceous genus not yet investigated. The similarity is enough to suggest that *Terebrirostra* should be assigned to the same subfamily as *Dereta*, i.e. Trigonoseminae.

TYPE SPECIMEN. The two specimens figured by d'Orbigny (1850 : pl. 519) were collected by Raulin and Buvignier. Buvignier's collection has not been traced and no specimens remotely like this species have been found in the Raulin Collection at the École des Mines, Paris. The selection of a possible neotype for the species, therefore, is still to be considered.

DISTRIBUTION. The type locality (d'Orbigny 1850) is in the Lower Albian beds of Grandpré, northeast of the Paris Basin, France, where, according to Peron (1905), it also occurs in the Upper Aptian 'sables ferrugineux'. As this information appears to have been obtained from mine workings, however, there is always the possibility of confusion over the horizon. The species also occurs in the Lower Albian

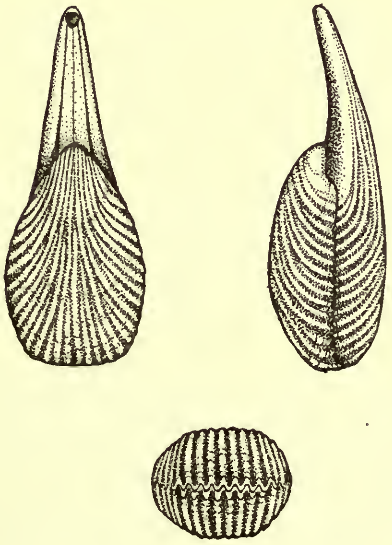

FIG. 27. The extraordinary extension of the umbo in *Terebrirostra* is a major point of distinction for the genus. The internal structures, as shown in the transverse serial sections (Fig. 28), can nevertheless be compared to those of *Dereta pectita* (Fig. 29). $\times 1\frac{1}{3}$.

Leymeriella tardifurcata Zone of the Shenley Limestone at Leighton Buzzard, Bedfordshire, where it was described by Walker (1903) as *Terebrirostra lyra* var. *incurvirostrum.*

REMARKS. Many of the brachiopod species described by Walker (1903) from the Shenley Limestone cannot be readily distinguished from species occurring in beds of equivalent age in the Lower Albian facies of Granpré and at Mont Saxonet, Perte du Rhône, Goudinière and Reposoir in the Haute Savoie, France. These include rhynchonelloid species and other terebratuloids and terebratelloids. Casey (1961) regarded the two species *T. arduenensis* and *T. incurvirostrum* as synonyms, but made no direct comparison of the two species with regard to the finer aspects of their morphology. We should remember there are certain minor differences in the general outline and costation of the two forms.

Genus ***DERETA*** Elliott 1959

TYPE SPECIES. *Terebratella pectita* (J. Sowerby 1816).

Dereta pectita (J. Sowerby 1816)

Fig. 29; Pl. 1, figs 8a–c.

1816 *Terebratula pectita* J. Sowerby: 83 ['87']; pl. 138, fig. 1.
1819 *Terebratula pectita* Sow.; Lamarck: 255.
1822 *Terebratella pectita* (Sow.) Brongniart & Cuvier: pl. 9, fig. 3.
1838 *Terebratula pectita* Sow.; von Buch: 168; pl. 16, fig. 12.
1848 *Terebratella pectita* (Sow.); d'Orbigny: 120; pl. 517, figs 16–20.
1852 *Terebratella pectita* (Sow.); Davidson: 26; pl. 3, figs 29–33.
1871 *Terebratula pectita* Sow.; Quenstedt: 267; pl. 44, figs 104–5.
1959 *Dereta pectita* (J. Sowerby) Elliott: 147.

DESCRIPTION. The species is variable, some forms developing a faint fold on the brachial valve with a corresponding sulcus in the pedicle valve. When these features occur with an extension of the hinge-line and more marked costae, it is very difficult to distinguish it from *Gemmarcula menardi* (Lamarck) with which it is sometimes associated. *Dereta pectita* remains subcircular in outline and is always more acutely biconvex than *G. menardi.* The costae, which are more numerous in *D. pectita,* are less deeply incised and appear more rounded in cross-section. They are given to more frequent bifurcation than in *G. menardi,* a feature which is more apparent at the margins.

The average length of the adult of the species is approximately 18 mm, width 17 mm and thickness 11 mm.

The dental lamellae in the pedicle valve appear early in development and remain strongly divergent, supporting subquadrate hinge-teeth. The cardinalia are well developed, extending into the the pedicle umbonal cavity in the early stages and gradually flattening. At the distal end of the cardinal process two plates develop and extend into the pedicle umbo, replacing the massive cardinal process. These plates are outward extensions of the hinge-plates which are fused anteriorly and

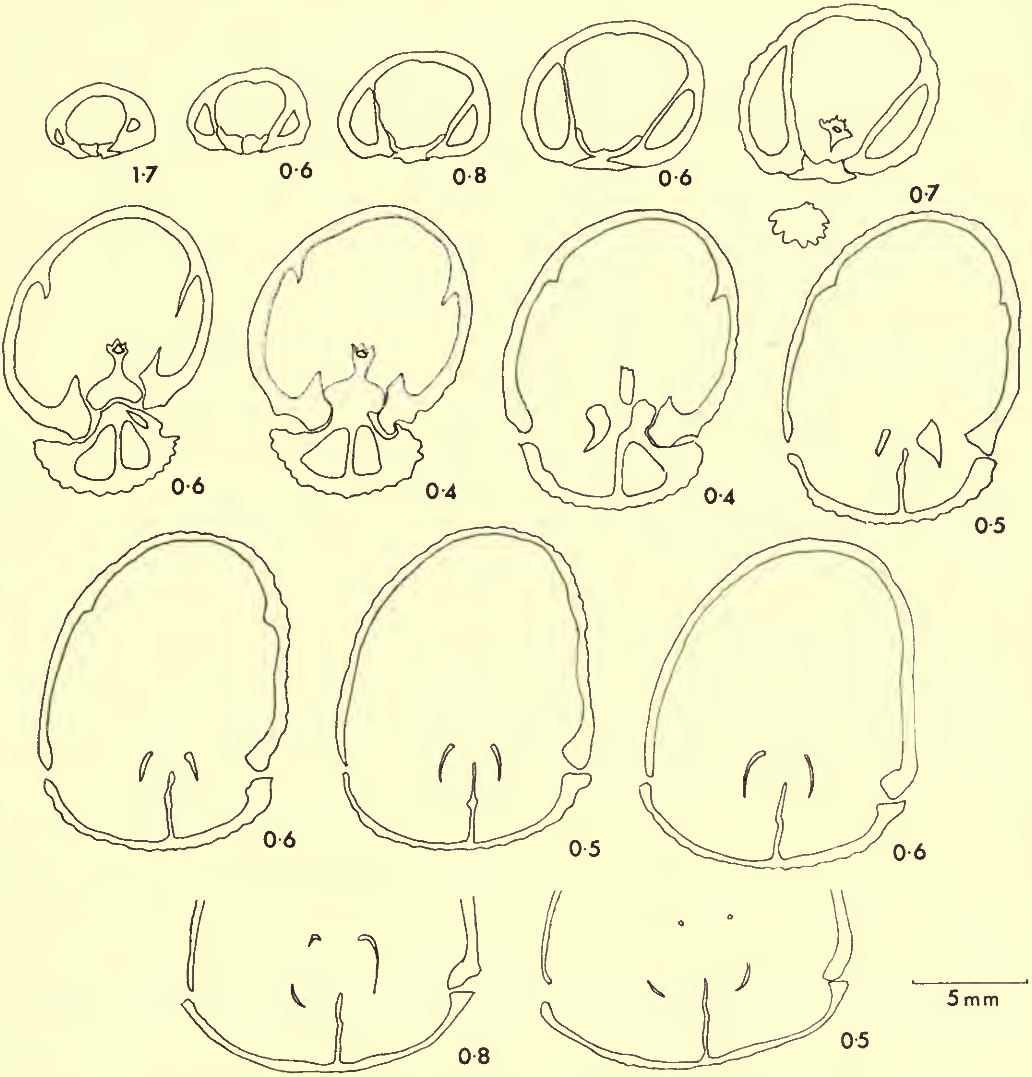

FIG. 28. Serial sections of *Terebrirostra bargesana* d'Orbigny show subtle points of distinction between this genus and *Dereta* (Fig. 29). Both series show similar extensions of the hinge-plates and poorly-developed hinge-trough. They also have a similar brachial loop pattern.

supported by a high persistent median septum from the floor of the brachial valve. The distal ends of this structure give rise to the descending branches of the brachial loop which remain close to the septum, elongating anteriorly to produce comparatively long crural processes.

HOLOTYPE. The specimen from the Upper Greensand of Horningsham, Wiltshire, in the Sowerby Collection, British Museum (Natural History), (B 61622)

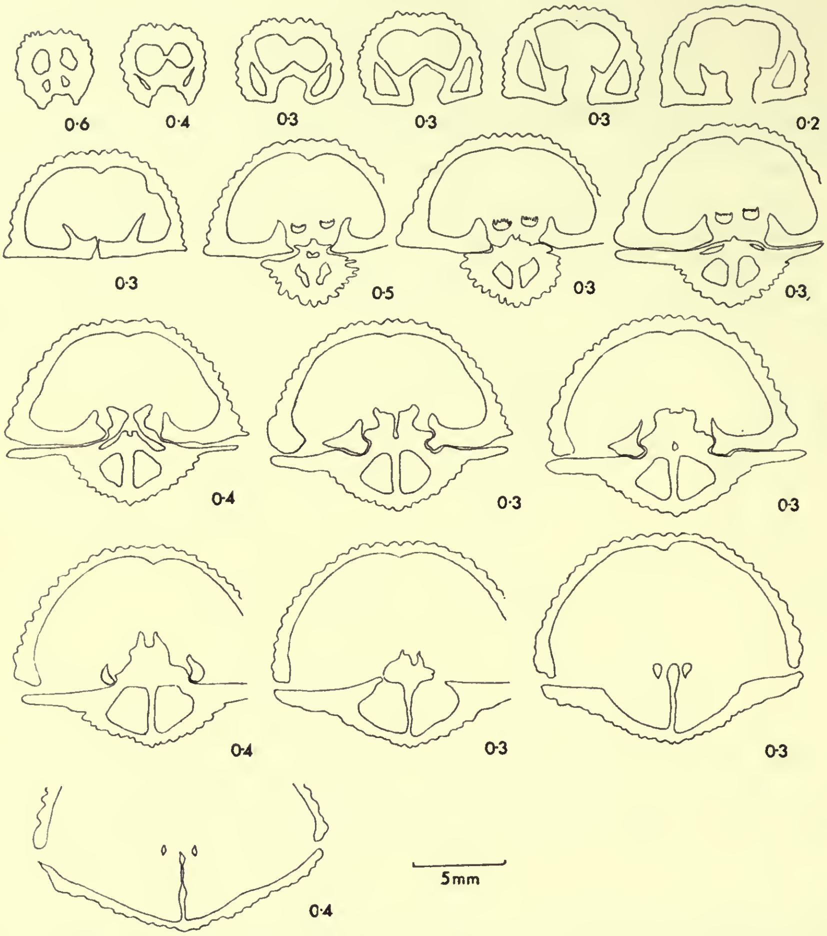

Fig. 29. *Dereta pectita* (J. Sowerby) seen in a series of 17 transverse sections. A well-marked pedicle collar, fused hinge-plates and high persistent median septum are clearly shown.

figured by J. Sowerby (1816: pl. 138, fig. 1). Dimensions: length 19·9 mm, width 20·0 mm and thickness 14·0 mm.

Distribution. Apart from the type locality near Warminster, Wiltshire, occurrences have been recorded from the Cenomanian Glauconitic Marl of Woody Bay, Binnell Point, Rocken End, Watershoot Bay and Compton Bay on the Isle of Wight, as well as from the Cenomanian Basement Bed of Swanage, Evershot and Melcombe Bingham in Dorset. Specimens have also been collected from the Upper Albian, *dispar* Zone, at Punfield Cove, Dorset.

In Europe the species appears to be confined to the Lower and Middle Cenomanian limestones of the Normandy coast, France.

REMARKS. In many ways *Dereta* and *Terebrirostra* have much in common. They share a similar geographical distribution and occur in very much the same lithologies, although not always together. They have very similar internal structures but may be distinguished by certain fundamental differences in the type of cardinal process. In *Dereta* this structure consists of a fusion of two separate parts, whereas in *Terebrirostra* it has been formed by the fusion of three distinct parts, as shown in the serial sections of the type species *T. lyra* given by Muir-Wood (1934 : 553) and the series shown here, Fig. 28, for *T. bargesana* (Pl. 3, figs 4a–c) from southern France. The extraordinary elongation of the umbo in *Terebrirostra* is also regarded as a point of distinction between the two genera.

Dereta can be distinguished from *Gemmarcula* in having a more highly complex and developed cardinal process, more clearly defined and persistent dental lamellae, and a more persistent and higher median septum.

IV. ACKNOWLEDGEMENTS

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PLATE 1

All specimens in Dept. of Palaeontology,
British Museum (Natural History).
a. Dorsal view. b. Lateral view. c. Anterior view.

Gemmarcula carantonensis (d'Orbigny) (p. 217)

FIGS 1a, b, c. Upper Cenomanian, Port des Barques, Charente, France. BB 45960. × 2.

Gemmarcula menardi (Lamarck) (p. 215)

FIGS 2a, b, c. Middle Cenomanian, near Le Mans, Sarthe, France. BB 35152. × 2.

Gemmarcula aurea Elliott (p. 211)

FIGS 3a, b, c. Upper Aptian, Sponge Gravel, Little Coxwell Pit, Faringdon, Berkshire. BB 45961. × 2.

Gemmarcula trifida (Meyer) (pp. 211, 217)

FIGS 4a, b, c. Upper Aptian, Brickhill, Bletchley, Buckinghamshire. BB 45962. × 2.

Ruegenella ciplyensis gen. et sp. nov. (p. 227)

FIGS. 5a, b, c. Upper Chalk, Craie Phosphatée, Ciply, Belgium. BB 45963. × 2.

Gemmarcula asteriana (d'Orb.) (pp. 214, 224 ; see also Pl. 2, figs 9a–c)

FIGS 6a, b, c. Aptian, Auxerre, Yonne, France. BB 45964. × 2.

Trigonosemus pectiniformis (von Buch) (p. 242)

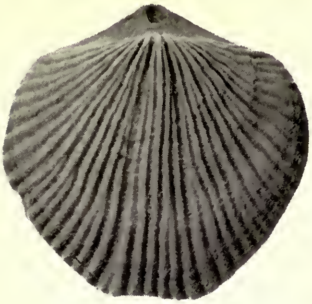
FIGS 7a, b, c. Upper Chalk, Maastrichtian, Maastricht, Netherlands. BB 45965. × 2.

Dereta pectita (J. Sowerby) (p. 246)

FIGS 8a, b, c. Middle Cenomanian, Warminster, Wiltshire. B 25263. × 2.

Ruegenella corneti (Hanstein) (p. 225)

FIGS 9a, b, c. Upper Chalk, Craie Phosphatée, Ciply, Belgium. BB 45966. × 1·5.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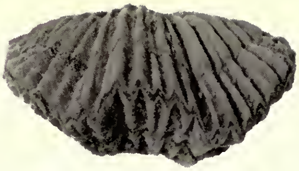
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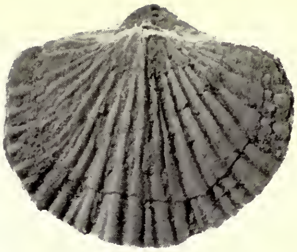
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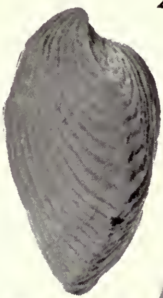
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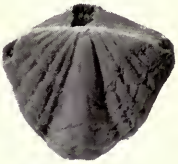
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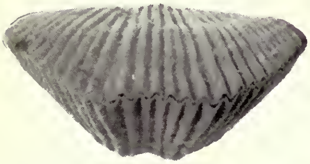
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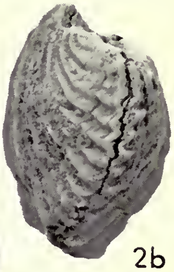
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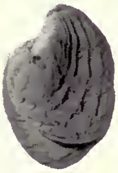
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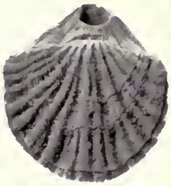
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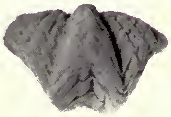
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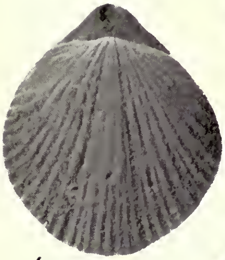
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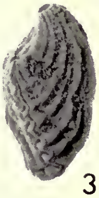
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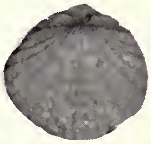
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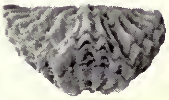
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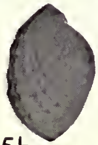
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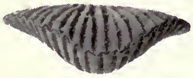
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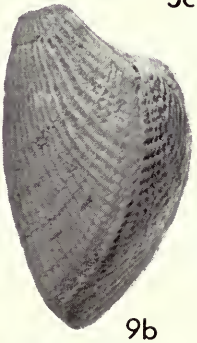
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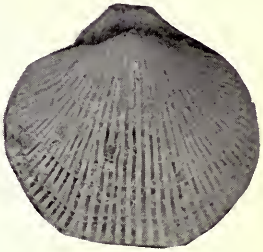
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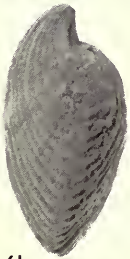
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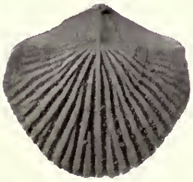
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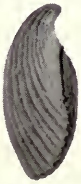
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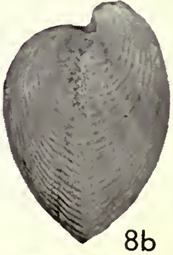
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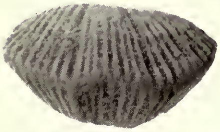
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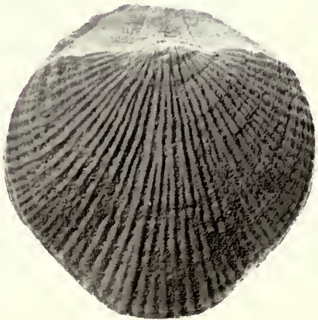
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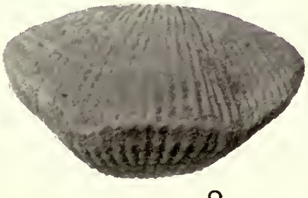
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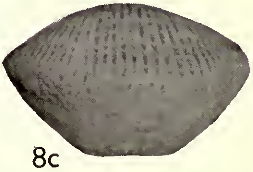
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PLATE 2

All specimens (except Figs 4) in Dept of Palaeontology,
British Museum (Natural History).
a. Dorsal view. b. Lateral view. c. Anterior view.

Gemmarcula pterygotos (Walker) (pp. 213, 221)

Figs 1a, b, c. Lower Albian, *L. tardefurcata* Zone, Munday's Hill, Leighton Buzzard, Bedfordshire. BB 45967. ×2.

Figs 2a, b, c. As above, showing numerous fine costae and thickened anterior margin. BB 45968. ×2.

Ismenia pectunculoides (Schlotheim) (p. 210)

Figs 3a, b, c. Upper Jurassic, Nattheim, Württemberg, Germany. B 86059. ×2.

Terebratella kofoedi Ravn (p. 221)

Figs 4a, b, c. Plaster cast. Middle Cenomanian, Madsegrav, Bornholm, Denmark. Original No. 1990 (Min. Geol. Mus. Univ. Copenhagen). ×2.

Helvetella arzierensis (de Loriol) (p. 222)

Figs 5a, b, c. Valanginian, Arzier, Vaud, Switzerland. BB 61527. ×2.

Arenaciarcula acuticostata sp. nov. (p. 238)

Figs 6a, b, c. Lower Albian, Munday's Hill, Leighton Buzzard, Bedfordshire. BB 45969. ×2.

Arenaciarcula beaumonti (d'Archiac) (p. 236)

Figs 7a, b, c. Tourtia, Tournai, Belgium. BB 45970. ×2.

Arenaciarcula fittoni (Meyer) (p. 235)

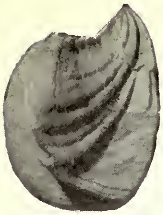
Figs 8a, b, c. Upper Aptian, Bargate Stone, Compton bypass, Surrey. B 95845. ×2.

Gemmarcula asteriana (d'Orbigny) (pp. 214, 224; see also Pl. 1, figs 6a–c)

Figs 9a, b, c. Aptian, Sardiniero, Santander, Spain. BB 45971. ×2.

Oblongarcula oblonga (J. de C. Sowerby) (p. 230; see also Pl. 3, figs 1a–c)

Figs 10a, b, c. Upper Aptian, Shanklin, Isle of Wight. BB 45972. ×2.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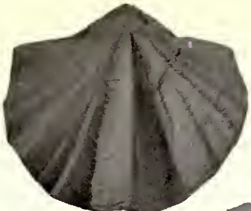
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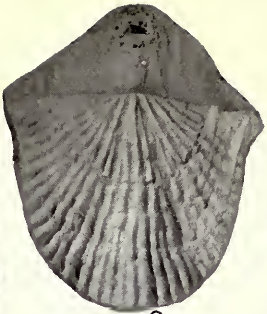
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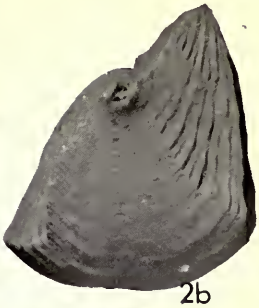
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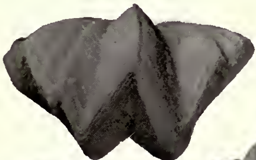
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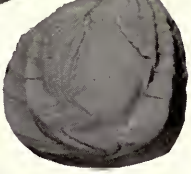
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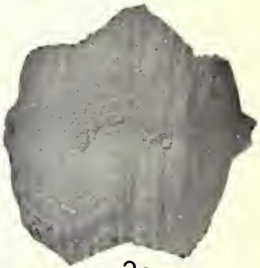
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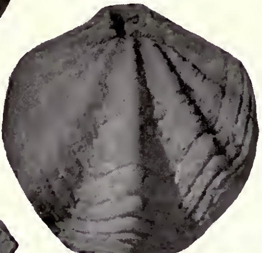
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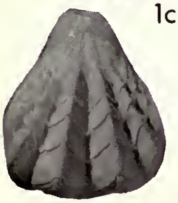
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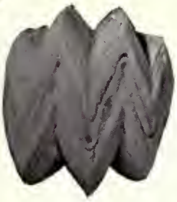
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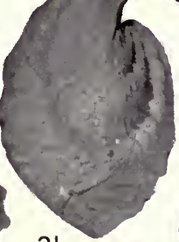
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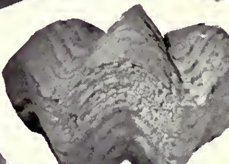
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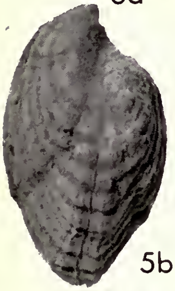
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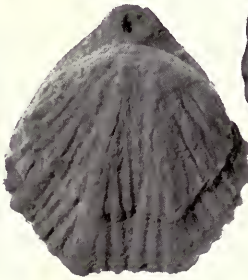
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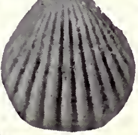
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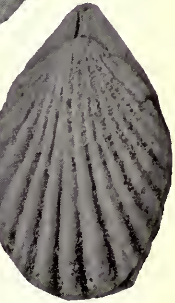
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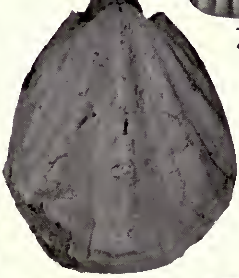
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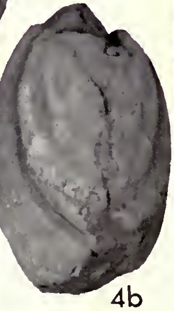
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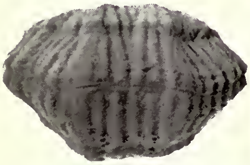
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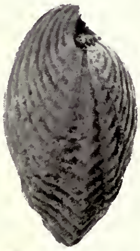
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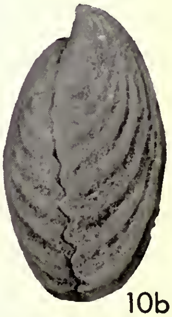
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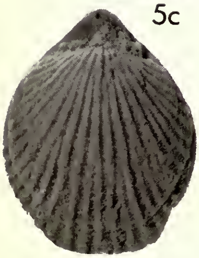
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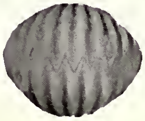
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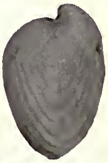
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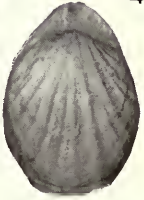
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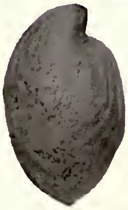
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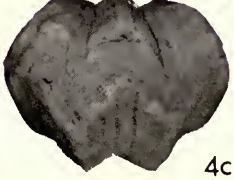
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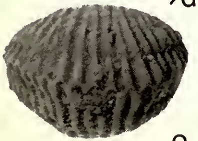
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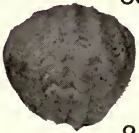
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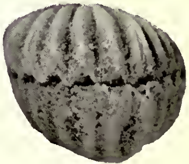
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PLATE 3

All specimens (except Figs 5–6) in Dept. of Palaeontology,
British Museum (Natural History)
a. Dorsal view. b. Lateral view. c. Anterior view.

Oblongarcula oblonga (J. de C. Sowerby) (p. 230 ; see also Pl. 2, figs 10a–c)

Figs 1a, b, c. Upper Aptian, Sponge Gravel, Faringdon, Berkshire. BB 45973. × 2.

Trigonosemus elegans Koenig (p. 241)

Figs 2a, b, c. Upper Chalk, Craie Phosphatée, Ciply, Belgium. BB 45974. × 2.

Arenaciarcula keepingi (Walker) (p. 240)

Figs 3a, b, c. Upper Aptian, Brickhill, Bletchley, Buckinghamshire. BB 45975. × 2.

Terebrirostra bargesana (d'Orbigny) (p. 249)

Figs 4a, b, c. Cenomanian, near La Bédoule, Bouches du Rhône, France. B 35187. × 1.

Oblongarcula alemannica sp. nov. (p. 227)

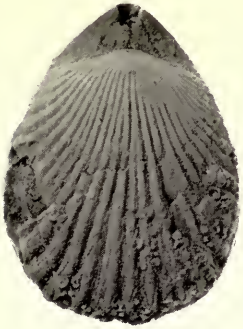
Figs 5a, b, c. Holotype. Hauterivian, Berklingen, north Germany. Roemer Mus. Hildesheim, No. RM 756. × 2.

Terebratella bornholmensis Ravn

Fig. 6. Plaster cast. Cenomanian, Madsegrav, Bornholm, Denmark. Original No. 1533 (Min. Geol. Mus. Univ. Copenhagen). × 2.

Oblongarcula davidsoni (Walker) (p. 233)

Figs 7a, b, c. Upper Aptian, Upware, Cambridge. BB 45976. × 2.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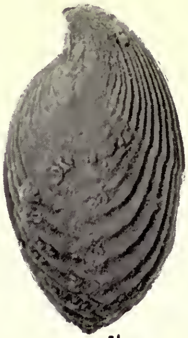
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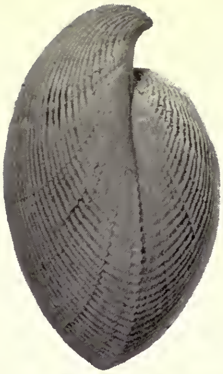
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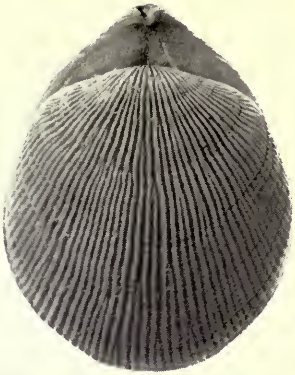
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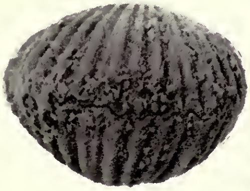
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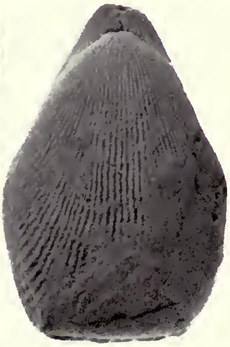
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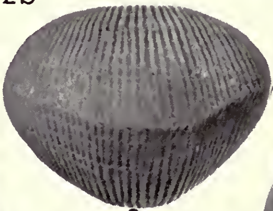
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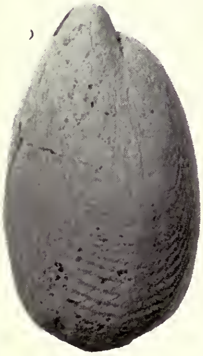
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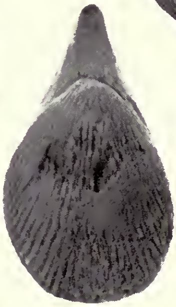
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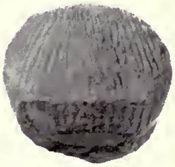
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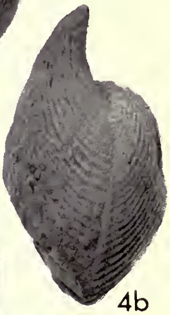
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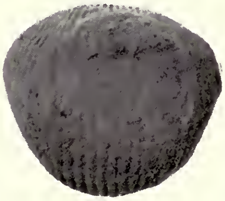
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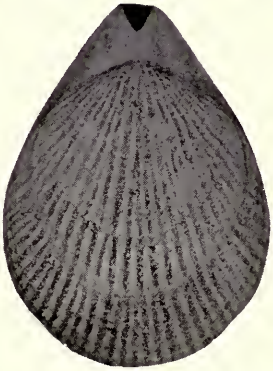
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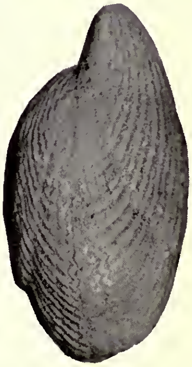
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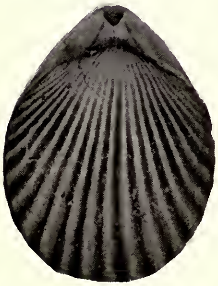
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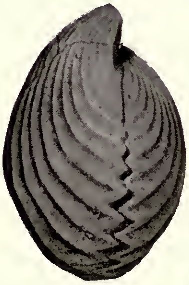
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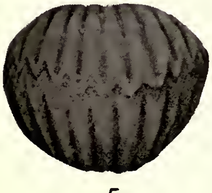
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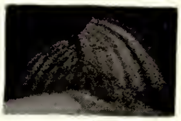
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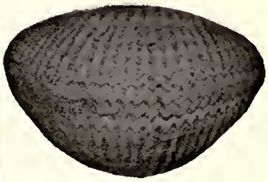
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A. N. FATMI

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GEOLOGY Vol. 28 No. 4
LONDON: 1977

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NEOCOMIAN AMMONITES FROM NORTHERN AREAS OF PAKISTAN

BY

ALI NASIR FATMI
Al Fateh University, Tripoli, Libya

Pp. 255–296 ; 12 *Plates* ; 1 *Text-figure*

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NEOCOMIAN AMMONITES FROM NORTHERN AREAS OF PAKISTAN

By A. N. FATMI

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ABSTRACT

Neocomian (Berriasian–Valanginian) ammonites from the Trans Indus Ranges in the Punjab Province and from the Samana Range and Khadimakh in Western Kohat, North West Frontier province of Pakistan, are described. The Berriasian is represented by the ammonite genera *Subthurmannia* (abundant), *Protacanthodiscus, Berriasella, Spiticeras* (*Spiticeras*), *Spiticeras* (*Negreliceras*), *Neocosmoceras, Bochianites* and *Neolissoceras*. Ammonites of Lower Valanginian age belong mostly to the genera *Thurmanniceras, Neocomites* (*Neocomites*), *Neocomites* (*Parandiceras*), *Neohoploceras, Sarasinella* and *Kilianella*. The Upper Valanginian is represented by abundant *Olcostephanus* (*Olcostephanus*), with *Olcostephanus* (*Rogersites*), *Neohoploceras, Lyticoceras, Leopoldia* and *Distoloceras*.

The Neocomian ammonites are distributed in the uppermost beds of the lower member and the whole of the middle member of the Chichali Formation. The rest of the lower member is Upper Jurassic while the upper member of the formation is devoid of ammonites in these areas.

The new species *Neocomites* (*Neocomites*) *copei* and *Neohoploceras collignoni* are erected, and new variants *isakhelensis* of *Olcostephanus* (*Rogersites*) *madagascariensis*, *surgharensis* of *Subthurmannia femori* and *noori* of *S. transitoria* proposed.

I. INTRODUCTION

AMMONITES of Neocomian (Berriasian–Valanginian) age are described from the Trans Indus Ranges (a westerly extension of the Salt Range) in the Punjab Province and from Western Kohat (Samana Range and its westerly extension into Khadimakh) in the North West Frontier Province of Pakistan (Fig. 1). A detailed account of the stratigraphy of the Jurassic and Lower Cretaceous rocks (including the Neocomian beds) and of the Jurassic ammonites from northern areas of Pakistan has been

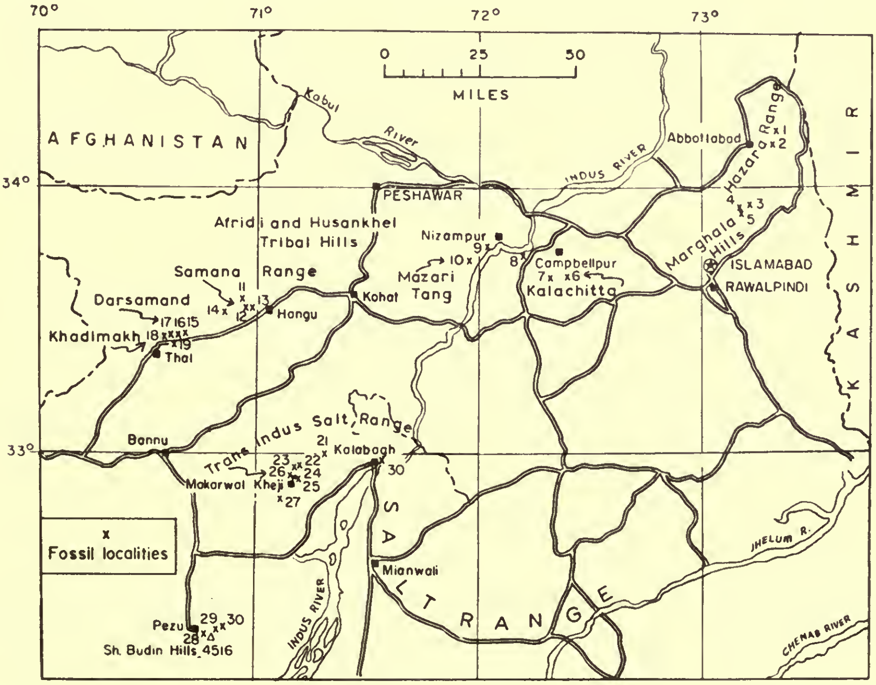
70°
71°
72°
73°
34°
33°
0 25 50
MILES
AFGHANISTAN
Kabul River
INDUS RIVER
Abbottabad
Hazara Range
1
2
3
4
5
PESHAWAR
Afridi and Husankhel Tribal Hills
Nizampur
9
10
8
Mazari Tang
Campbellpur
7
6
Kalachitta
Margala Hills
ISLAMABAD
RAWALPINDI
KASHMIR
Samana Range
11
13
12
14
Darsamand
17 16 15
Hangu
Kohat
Khadimakh
18
19
Thal
Trans Indus Salt Range
Bannu
21
22
23
26
24
25
27
Kalabagh
30
Makarwal
Kheji
SALT RANGE
Mianwali
INDUS RIVER
JHELUM R.
CHENAB RIVER
x
Fossil localities
Pezu
28
29
30
Sh. Budin Hills 4516

FIG. 1. Fossil locality map of Hazara, Kala Chitta, Kohat, Trans Indus Ranges and Shaikh Budin Hills, Pakistan.

already published (Fatmi 1972). This paper is a sequel and deals only with the systematic descriptions of the Neocomian ammonites from the Chichali Formation.

The most important contributions to knowledge of the ammonite faunas of this region are by Spath (1930, 1939), who described in detail the cephalopods of the Neocomian Belemnite Beds of the Salt Range (1939) and established some important genera and many new species from this region. In 1930 he had established the presence of Neocomian beds at Khadimakh in Western Kohat on an *Olcostephanus* fragment collected by Davis (1930) from Khadimakh. The ammonites described in the present paper were collected from some localities known to Spath in the western extension of the Salt Range, and from newly discovered localities and horizons. The ammonites of Berriasian and Upper and Lower Valanginian age from the Samana Range and Khadimakh in Western Kohat are recorded for the first time. The discussion of Neocomian ammonites from the Trans Indus Ranges, mainly a revision of Spath's work, includes some forms not recorded before, and there is new information on the stratigraphic position of the faunas within the Chichali Formation which was not precisely known previously.

This paper forms a part of the author's Ph.D. thesis submitted to the University of Wales (University College of Swansea) in 1968. Since the publication of the major part of the thesis (Fatmi 1972) the Neocomian ammonites have been revised and brought up to date. Many colleagues and friends in and outside Pakistan have already been acknowledged (Fatmi 1972 : 305). For this paper I am deeply indebted to Dr M. K. Howarth for his guidance and critical review of the fauna and text. Sincere thanks are also due to Dr P. F. Rawson of Queen Mary College, London, who through the courtesy of Dr Howarth reviewed the identifications and offered many useful suggestions. Mr D. Phillips and other members of staff of the Department of Palaeontology of the British Museum (Natural History) are thanked for reorganizing and photographing the specimens.

The systematic descriptions mostly carry the standard morphological terms as defined in Part L of the *Treatise on Invertebrate Paleontology* (Arkell *et al.* 1957). The standard dimensions (diameter, whorl height, whorl breadth, umbilical width) are given in millimetres and as percentages of the diameter. Stratigraphical field measurements are given in feet as originally made (Fatmi 1972 : 302) with approximate metric conversions.

II. STRATIGRAPHIC SUMMARY

Neocomian ammonites occur in the Chichali Formation of Upper Jurassic to Lower Cretaceous age. The name Chichali Formation was introduced by Danilchik (1961) and Danilchik & Shah (1967), from the Chichali Pass in the Trans Indus Ranges, and it has since been approved by the Stratigraphic Committee of Pakistan for rocks previously referred to as 'Belemnite Beds' and 'Belemnite Shale' (Davies 1930, Spath 1939, Gee 1945, Pascoe 1959, Krishnan 1960).

The stratigraphic position of the formation in the area is as follows.

Lumshiwal Formation (Sandstone)	Lower Cretaceous (Aptian to Albian)
Chichali Formation (glauconitic sandstone and sandy shale)	Upper Jurassic to Neocomian
∼∼∼∼∼∼∼∼ DISCONFORMITY	∼∼∼∼∼∼∼∼
Samana Suk Limestone (Limestone and Marl)	Middle Jurassic

The Chichali Formation (for details see Fatmi 1972) consists of dark green to dark greenish grey (weathering partly as rusty brown to purple) sandstones and sandy shales which are glauconitic and chamositic and include calcareous, phosphatic, silty concretions, lenses and nodules. Most of the ammonites occur in nodules and are mainly preserved as internal moulds, but some have recrystallized shell material.

The Chichali Formation is divisible into three members in the Trans Indus and Samana Ranges, but at Khadimakh the upper member is similar to the overlying Lumshiwal Formation in lithology and thus only the lower two divisions are recognizable. The thickness of the formation varies from a maximum 185 feet (56 m) in section in the Trans Indus Ranges to a minimum of 50 feet (15 m) in Western Kohat. The three members are as follows.

Upper	Soft sandstone and sandy shale, glauconitic and chamositic, poor in fossils.	25–60 feet (7½–18 m)
Middle	Sandstone, massive, rusty brown to greenish, glauconitic, calcareous, phosphatic, with frequent ammonites and abundant belemnites (*Hibolithes*).	20–30 feet (6–9 m)
Lower	Soft sandstone and sandy shale, dark green to dark greenish grey, glauconitic with ammonites and abundant belemnites.	7–75 feet (2–23 m)

The Neocomian ammonites occur in the middle member and the upper part of the lower member of the formation. The upper member is poor in fossils (excepting for some bivalves and a few *Hibolithes*) and is regarded as Upper Neocomian (post-Valanginian). The rest of the lower member has an Upper Jurassic fauna. The Berriasian ammonites occur in the upper 2 to 3 feet (c. ¾ m) of the lower member and basal 3 to 4 feet (c. 1 m) of the middle member; the rest of the middle member contains the Valanginian fauna.

III. FAUNAL SUMMARY

Since the presentation of the thesis (1968) and the publication of my earlier paper (Fatmi 1972) a revision of the Neocomian faunas has been made. This has necessitated changes in the identification of a few forms I referred to previously (1972 : 319, 320, 362 ; fig. 6) ; the correct identification of these ammonites should now be taken as follows.

1. *Neocomites* (*Odontodiscoceras*) *similis* Spath to be regarded as *Neocomites* (*N.*) *similis* Spath (p. 280).
2. *Neocomites* (*Parandiceras*) *theodorii* (Oppel) and *Neocomites* (*P.*) aff. *indicus* (Uhlig) are to be regarded as variants of *N.* (*P.*) *rota* Spath (p. 282).
3. *Kilianella* sp. nov. is now considered to be *Neocomites* (*N.*) *campylotoxus* (Uhlig) (p. 279).
4. *Subthurmannia* forms referred doubtfully to *S. boissieri* (Pictet) and *S. pseudopunctata* Spath are regarded now as sp. indet. (p. 275).
5. The 'subspecies' of *Olcostephanus* (*O.*) *salinarius* Spath referred to previously are treated now as variants (p. 266).
6. Forms referred to *Olcostephanus* (*O.*) cf. *filosa* (Baumburger) and *O.* (*O.*) aff. *geei* Spath are included in *O.* (*O.*) *sakalavensis* (Besairie) (p. 267).
7. The specimen referred to *Olcostephanus* (*Rogersites*) sp. nov. is now regarded as a new variant of *O.* (*R.*) *madagascariensis* Lemoine (p. 272).
8. The globular forms referred to *Olcostephanus* (*O.*) *pachycyclus* Spath are included in *O.* (*O.*) *globosus* Spath (p. 270).
9. Some species referred previously to the subgenus *Calliptychoceras* are included in the subgenus *Neocomites* (p. 279).

The Berriasian forms which occur in the basal middle and uppermost lower members of the Chichali Formation include species of the genera *Subthurmannia* (abundant), *Berriasella, Protacanthodiscus, Spiticeras* (*Spiticeras*), *Spiticeras* (*Negreliceras*), *Bochianites* and *Neolissoceras.*

The Lower Valanginian (middle member of the Chichali Formation) is represented by *Thurmanniceras, Sarasinella, Neocomites* (*Neocomites*), *Neocomites* (*Parandiceras*), *Uhligites, Kilianella* and *Neohoploceras.*

The Upper Valanginian fauna occurs in the upper 2 to 3 feet (c. $\frac{3}{4}$ m) of the middle member of the Chichali Formation and consists of *Olcostephanus* (*Olcostephanus*) (abundant), *O.* (*Rogersites*), *Neohoploceras, Leopoldia, Distoloceras* and *Lyticoceras.*

IV. SYSTEMATIC DESCRIPTIONS

Class *CEPHALOPODA*

Sub-class *AMMONOIDEA*

Order LYTOCERATIDA

Superfamily **ANCYLOCERATACEAE** Meek 1876

Family **BOCHIANITIDAE** Spath 1922

Genus ***BOCHIANITES*** Lory 1898

Bochianites cf. ***gerardianus*** (Stoliczka 1866)

1866 *Anisoceras gerardianum* Stoliczka : 110 ; pl. X, fig. 3.
1910 *Bochianites gerardianus* (Stoliczka) Uhlig : 381 ; pl. LXXIX, figs 3a–f.

Material. One specimen, C.79100.

Horizon. Lower part of the middle member of the Chichali Formation; Berriasian.

Remarks. The specimen (a body chamber fragment) has an oval whorl section and simple strongly prorsiradiate ribs which cross the venter with forward arching but are weak along the siphonal line. There is one prorsiradiate constriction at the adoral end. The specimen closely resembles the holotype from Spiti, Himalaya, which was refigured by Uhlig (1910). It is reported for the first time from the Trans Indus Ranges.

Locality. Lunda Mines, Trans Indus Ranges.

Order AMMONITIDA
Superfamily **HAPLOCERATACEAE** Zittel 1884
Family **HAPLOCERATIDAE** Zittel 1884
Genus ***NEOLISSOCERAS*** Spath 1923
Neolissoceras grasianum (d'Orbigny 1841)
Pl. 1, figs 1, 2

1841 *Ammonites grasianus* d'Orbigny : 141 ; pl. XLIV.
1939 *Neolissoceras grasianum* (d'Orbigny) Spath : 8 ; pl. I, figs 4a–d (with synonymy).

Material. Four specimens, C.79101–4.

Horizon. Basal middle and top of lower members of the Chichali Formation in the Trans Indus Ranges, and lower part of dark rusty brown member of the Chichali Formation at Khadimakh (Western Kohat); Berriasian.

Description. The figured specimens are septate and have an involute, smooth shell. The whorl section is subrectangular with flat to gently concave flanks and broadly arched venter. The umbilicus is narrow and has a well-defined umbilical shoulder with a slanting umbilical wall.

Dimensions. C.79101 – 50 : 25·0 (50%), 15·8 (31%), 9·5 (19%).
C.79102 – 28 : 14·0 (50%), 9·0 (32%), 5·5 (19%).

Remarks. Spath (1939) figured a similar form from the Trans Indus Range, and assigned to it a Valanginian age. The specimens figured here were collected from a stratigraphic horizon that has yielded *Subthurmannia*, suggesting a Berriasian age. It is very likely that Spath's specimens (collected by other workers) also came from the present level.

Localities. Chichali Pass, Punnu Mines, south-west of Malla Khel in the Trans Indus Ranges, and Khadimakh in Western Kohat.

Family **OPPELLIDAE** Bonarelli 1894
Subfamily **STREBLITINAE** Spath 1925
Genus ***UHLIGITES*** Kilian 1907
Uhligites sp. indet.

Material. One specimen, C.79105.

Horizon. About 7 feet (2 m) below the top of the middle member of the Chichali Formation; Valanginian.

Remarks. The specimen, which is poorly preserved, is of moderately large size (240 mm diameter) and has an oxyconic, very involute shell. The whorl section is compressed, with gently arched flanks which are convergent towards an acutely rounded to subtabulate venter. The suture line is highly complex.

Locality. South-west of Malla Khel, Trans Indus Ranges.

Superfamily **PERISPHINCTACEAE** Steinmann 1890
Family **OLCOSTEPHANIDAE** Haug 1910
Subfamily **SPITICERATINAE** Spath 1924
Genus ***SPITICERAS*** Uhlig 1903
Subgenus ***SPITICERAS*** Uhlig 1903
Spiticeras (Spiticeras) cf. ***griesbachi*** (Uhlig 1903)
Pl. 1, fig. 4

1903 *Holcostephanus* (*Spiticeras*) *griesbachi* Uhlig : 115 ; pl. XI, figs 3a–d.

Material. One specimen, C.79106.

Horizon. Upper part of the lower member of the Chichali Formation in the Samana Range, Western Kohat; Berriasian.

Description. The septate specimen has an evolute shell, an oval whorl section (whole height 35 mm and whole breadth 30 mm), with flattish flanks and an evenly rounded venter. The umbilicus is wide. The umbilical wall is rounded. Prominent constrictions are present. The ribs are slightly prorsiradiate and cross the venter with a forward swing, and are bundled rather irregularly at prominent umbilical tubercles. Branching of ribs takes place at the umbilical shoulder and slightly below the middle of the flank.

Remarks. The figured specimens compare favourably in ornamentation and whorl section with the holotype from Lochambelkichak, Spiti. In ornamentation it may be compared with *Spiticeras* (*S.*) *scriptus* (Strachey) figured by Uhlig (1910 : pl. XV, figs 1a–g ; pl. LVIII, figs 2a–c) but differs in having a more elevated whorl section and prominent bullae. The species is recorded for the first time from the Samana Range.

Locality. South of Fort Lockhart, Samana Range.

Spiticeras (Spiticeras) mojsvari (Uhlig 1903)
Pl. 1, fig. 3

1903 *Holcostephanus* (*Spiticeras*) *mojsvari* Uhlig : 110 ; pl. XVII, figs 1a–d.

Material. One specimen, C.79107.

Horizon. Lower part of rusty brown sandstone member of the Chichali Formation at Khadimakh, Western Kohat ; Berriasian.

Description. The specimen is septate and has a moderately evolute and inflated shell. It has a whorl height of 33 mm and whorl thickness of 36 mm. The flanks are subparallel on the lower half but arched and convergent on the upper half, and the venter is arched. The umbilical wall is almost vertical. One deep constriction is present.

The straight, prorsiradiate ribs swing forwards across the venter, but are weak on the siphonal line. They are bundled at prominent blunt umbilical bullae. The ribs also bifurcate higher up on the flank.

Remarks. The figured specimen compares favourably with Uhlig's holotype from Lochambelkichak, Spiti, which at 114 mm diameter has a whorl height of 33 mm and whorl breadth of 45 mm. It may also be compared with *Spiticeras* (*Spiticeras*) *scriptus* (Strachey) as figured by Uhlig (1910 : pl. LVIII, figs 2a–c ; pl. XV, figs 3a–d), but it differs in having more compressed whorls and more ribs.

Locality. Khadimakh (south flank), Kohat district.

Subgenus **NEGRELICERAS** Djanélidzé 1922

Spiticeras (Negreliceras) tenuicostatum Djanélidzé 1922

Pl. 2, fig. 2

1922 *Spiticeras* (*Negreliceras*) *tenuicostatum* Djanélidzé : 106 ; pl. VII, figs 4, 5.

1939 *Spiticeras* (*Negreliceras*?) sp. nov. aff. *subnegreli* Djanélidzé ; Spath : 38 ; pl. II, figs 9a–d.

Material. Three specimens, C.79108–10.

Horizon. Basal part of the middle member of the Chichali Formation ; Berriasian.

Description. The shell is rather involute, compressed and approximately 150 mm in diameter. The whorl section is elliptical, much higher than wide on the outer whorl and less so on the inner whorls. The flanks are flat, convergent towards a rounded venter, and the maximum thickness is near the umbilical shoulder. The umbilical wall is steeply inclined. Constrictions, more prorsiradiate than the ribs, are present on the inner whorl fragments.

The ribs are dense and rather weak on the lower half of the flank and the venter, but prominent on the upper half of the flank. The primary ribs are coarse, rursiradiate on the umbilical wall, but recurve to become rectiradiate, and swell into elongated blunt tubercles at the umbilical shoulder and lowermost part of the flank. At 150 mm diameter the prorsiradiate primary ribs extend to about the middle of the flank, and on the upper half of the flank they give place to sheaves of 2 to 4 secondary ribs which are bundled irregularly. Less commonly the branching of ribs also takes place irregularly on the lower third of the flank and at the umbilical shoulder. In addition there are some irregular intercalatory ribs which extend about half way down on the flank. All the ribs are moderately prorsiradiate, are projected further forwards on the venter but weaken along the siphonal line. There are 13 primary ribs and tubercles per half whorl at 150 mm diameter.

Dimensions. C.79108 – c. 150·0, c. 58·0 (39%), ? 36·0 (25%), 48·0 (32%).

Remarks. The species differs from S. (*Negreliceras*) *subnegreli* Djanélidzé in being much more involute, in having a more elevated whorl section, and different rib style at a larger diameter. The inner whorl fragments also show a less compressed whorl section with greater whorl breadth. There is, however, strong resemblance in ventral and side view, particularly in the forward projection of ribs near the ventral margin and on the venter. The number and nature of the primary ribs and umbilical tubercles are also very similar.

In whorl section the species is comparable with S. (*Negreliceras*) *ducalis* (Matheron 1880 : pl. B27, figs 2a–b) but differs in being more involute and in having a different rib style at a comparative diameter.

Spath (1939 : pl. II, figs 9a–d) described a fragmentary specimen from a nearby locality in the Trans Indus Ranges as *Spiticeras* (*Negreliceras*) sp. nov. aff. *subnegreli* Djanélidzé. The inner whorl fragments of the described species are very similar to Spath's form and because of their greater involution may belong to S. (*Negreliceras*) *tenuicostatum*.

Localities. South-west of Malla Khel and Punnu Mines, Trans Indus Ranges.

Subfamily **OLCOSTEPHANINAE** Haug 1910

Genus ***OLCOSTEPHANUS*** Neumayr 1875

Subgenus ***OLCOSTEPHANUS*** Neumayr 1875

Olcostephanus (Olcostephanus) salinarius Spath 1939

Pl. 1, figs 5, 6 ; Pl. 2, fig. 4 ; Pl. 3, fig. 1

1930 *Olcostephanus* aff. *astierianus* (d'Orbigny) Spath : 58 ; pl. VII, figs 4, 5.
1939 *Olcostephanus salinarius* Spath : 13 ; pl. I, figs 1a–b, 8a–b.
1972 *Olcostephanus* (*Olcostephanus*) *salinarius* subspp. ; Fatmi : 319–20.

Material. Fifteen specimens, C.79111–25.

Horizon. Upper part of the middle member of the Chichali Formation in the Trans Indus Ranges and Samana Range, and the upper part of the rusty brown sandstone member of the Chichali Formation at Khadimakh (Western Kohat) ; Upper Valanginian.

Description. The collection contains 7 complete adult specimens in which all or part of the flared mouth border is preserved ; four of them have large triangular lateral lappets at their final diameters of 93, 82, 81 and 53 mm ; the other three are c. 83, 80 and c. 64 mm in diameter at their apertures, but their mouth borders are partly broken away and lappets are not preserved. The modifications at the aperture (Pl. 1, fig. 5 ; Pl. 2, fig. 4) start with a highly oblique flared rib followed by a constriction, then the mouth border itself consisting of a large lateral projection between the umbilical seam and the middle of the whorl side, the large triangular lappet on the upper half of the whorl side, and a large rib over the venter projecting upwards. The adult body chamber is about $\frac{3}{4}$ of a whorl long. All these specimens are microconchs. The other 8 specimens are smaller and incomplete.

The shell is involute and has a depressed rounded whorl section, with steep but rounded umbilical walls. The primary ribs are strongly rursiradiate on the umbilical slope and give place to radially elongated tubercles at the umbilical edge. Bundles of 3 to 5 ribs issue from the tubercles; they are prorsiradiate on the middle of the flanks then recurve to rectiradiate or gently rursiradiate on the upper part of the flanks and across the venter. Occasionally there are intercalated secondary ribs.

DIMENSIONS. C.79111 – 60·0 : 24·0 (40%), 28·5 (48%), 19·0 (32%).
C.79114 – 42·0 : 18·0 (43%), 24·0 (57%), 12·0 (29%).
C.79116 – 79·0 : 32·0 (41%), 4·0 (51%), 26·5 (34%).
C.79117 – 48·0 : 18·0 (38%), 25·5 (53%), 16·5 (34%).
C.79118 – 80·0 : 32·0 (40%), 38·0 (48%), 22·5 (28%).
C.79120 – 86·0 : 34·0 (40%), 40·0 (47%), 24·5 (28%).
C.79121 – 33·0 : 14·5 (44%), 20·0 (61%), 10·0 (30%).
C.79122 – 55·0 : 19·0 (35%), 30·5 (55%), 20·5 (37%).

REMARKS. *Olcostephanus* (*O.*) *salinarius* Spath is the most common species of the genus in the Trans Indus Ranges, and has been recognized from the Samana Range and Khadimakh in Western Kohat. The species shows a fair range of variation in the density and strength of the primary and secondary ribs, the lateral tubercles and in involution, which made Spath recognize a number of variants of the species. Var. *crassa* (Spath 1939 : pl. I, fig. 3) is characterized by fewer secondary ribs and greater whorl inflation, while var. *obesa* (Spath 1939 : pl. II, fig. 5) is characterized by a more evolute shell. Spath's two other varieties, namely *involuta* (1939 : pl. I, fig. 2) and *subfilosa* (1939 : pl. I, fig. 6) are more closely related to *Olcostephanus* (*O.*) *sakalavensis* (Besairie 1936 : 139; pl. XIII, figs 10–12) because of their more involute shells, weaker primary ribs and umbilical tubercles, and finer secondary ribs.

The holotype figured by Spath (1939 : pl. I, fig. 1) has lappets at its mouth border at 70 mm diameter, and three other specimens figured by him have mouth borders and lappets at c. 71, 69 and 60 mm diameter. All the known adults of *O. salinarius* are thus microconchs ranging from 53 to 93 mm diameter; the accompanying macroconchs are not known, though it is possible that they may be those specimens described below as *O. fascigerus* and *O. sublaevis*.

LOCALITIES. Many localities in the Trans Indus and Samana Ranges, and Khadimakh in Western Kohat.

Olcostephanus (Olcostephanus) sakalavensis (Besairie 1936)

Pl. 2, figs 1, 3; Pl. 3, fig. 2; Pl. 4, fig. 3

1936 *Rogersites sakalavensis* Besairie : 139; pl. XIII, figs 10–12.
1939 *Olcostephanus sakalavensis* (Besairie) Spath : 138; figs 5a–b.
1939 *Olcostephanus salinarius*, varieties *subfilosa* and *involuta* Spath : 13; pl. I, figs 2, 6a–b; pl. II, fig. 4.
1939 *Olcostephanus victoris* Spath : 20; pl. XIX, figs 7a, b.
1939 *Olcostephanus geei* Spath : 26; pl. VII, figs 5–6.
1972 *Olcostephanus* (*Olcostephanus*) cf. *filosa* (Baumberger); Fatmi : 320.
1972 *Olcostephanus* (*Olcostephanus*) aff. *geei* Spath; Fatmi : 320.

Material. Ten specimens, C.79126–35.

Horizon. Top bed of the middle member of the Chichali Formation in the Trans Indus Ranges, and top bed of the rusty brown sandstone member at Khadimakh, Western Kohat ; Valanginian (Upper).

Description. The species is represented by a number of septate specimens of moderate size and involution. The whorl section is subcircular to oval, wider than high with arched flanks and venter. The umbilicus is narrow and deep, with a steep umbilical wall and rounded shoulder.

The ribs are rursiradiate on the umbilical wall and swell into small rather weak tubercles at the umbilical edge. Coming from these tubercles are bundles of 4 to 7 fine ribs which are prorsiradiate on the flanks then recurve to become rectiradiate across the venter. A few ribs occasionally bifurcate higher up on the flank and there are occasional intercalated ribs.

Dimensions. C.79126 – 54·0 : 24·0 (44%), 28·0 (52%), 13·0 (24%).
C.79127 – 87·0 : 42·0 (48%), 47·0 (54%), 18·0 (21%).
C.79131 – 48·0 : 20·0 (42%), 30·0 (63%), 13·0 (27%).
C.79132 – 55·0 : 27·0 (49%), 30·0 (64%), 10·5 (19%).

Remarks. *Olcostephanus* (*O.*) *sakalavensis* (Besairie) differs from *O.* (*O.*) *salinarius* Spath in being more involute, more finely and densely ribbed, and in having smaller and weaker umbilical tubercles.

The varieties *subfilosa* and *involuta* described by Spath (1939 : 13 ; pl. I, figs 6a–b ; pl. I, fig. 2 ; pl. II, fig. 4) under *Olcostephanus salinarius* Spath seem to be more closely related to *O. sakalavensis* (Besairie) in their weaker umbilical tubercles, finer ribs and greater involution than *salinarius*. *Olcostephanus* (*O.*) *victoris* Spath (1939 : 20 ; pl. XIX, figs 7a, b) (dimensions : 105, 43%, 54%, 26%) and *Olcostephanus* (*O.*) *geei* Spath (1939 : 26 ; pl. VII, figs 5, 6) (dimensions : 65, 46%, 60%, 20%) are considered here as synonyms of *O. sakalavensis* (Besairie), for both specimens are finely ribbed and have weaker lateral tubercles similar to those of *O. sakalavensis*.

The species is second in order of abundance to *O. salinarius*, and is reported for the first time from the Western Kohat and Trans Indus Ranges.

Localities. Chichali Pass, south-west of Malla Khel, Makerwal in the Trans Indus Ranges and south of Khadimakh in Western Kohat.

Olcostephanus (Olcostephanus) fascigerus Spath 1939

Pl. 3, fig. 3

1939 *Olcostephanus fascigerus* Spath : 18 ; pl. IV, figs 1–3.

Material. One specimen, C.79136.

Horizon. Top bed of the middle member of the Chichali Formation ; Valanginian (Upper).

Description. The whorl section is depressed, subcircular, with arched flank and venter. The umbilicus is narrow and has a steep, high, curved umbilical wall and rounded umbilical shoulder. Shallow constrictions are present.

The ribs are rursiradiate or rectiradiate on the umbilical wall, and at the umbilical shoulder they give way to sharp elongated tubercles. Derived from these tubercles are bundles of 4 to 6 ribs which are prorsiradiate on the flanks, then recurve to rectiradiate across the venter. One or two secondary ribs are intercalated. Approximately 14 primary and 70 secondary ribs are present at 90 mm on the half whorl specimen.

DIMENSIONS. C.79136 – 90·0 : 39·0 (43%), 53·0 (59%), 22·5 (25%).

REMARKS. The specimen compares closely in ornamentation and dimensions with Spath's holotype, which at 110 mm diameter has nearly half a whorl of body chamber. The Pakistani species is allied to *O. uitenhagensis* Kitchin (1908 : 206 ; pl. XI) and *O. rabei* (Besairie) (1936 : 141 ; pl. XII, figs 8, 9) but differs in being more evolute and inflated.

LOCALITY. Makerwal in the Trans Indus Ranges.

Olcostephanus (Olcostephanus) sublaevis Spath 1939

Pl. 4, fig. 2

1939 *Olcostephanus sublaevis* Spath : 21 ; pl. III, figs 1–3 ; pl. XIX, fig. 2.

MATERIAL. Four specimens, C.79137–40.

HORIZON. Upper part of the middle member of the Chichali Formation in the Trans Indus Ranges, and upper bed of the rusty brown sandstone member of the Chichali Formation at Khadimakh, Western Kohat ; Valanginian (Upper).

DESCRIPTION. The figured specimen is involute, inflated, semi-globular, septate and 114 mm in diameter. The whorl section is depressed and has evenly arched venter and flanks which meet the umbilical wall in a well-rounded shoulder. The umbilicus is narrow and deep, and has steep walls.

The ribs are weak and rursiradiate on the umbilical wall, and at the umbilical shoulder they swell into prominent bullae. Coming from these tubercles are bundles of 4 to 6 ribs which are prorsiradiate at first, then recurve to rectiradiate across the venter. Occasional ribs are intercalated. There is slight weakening of the ribs along the siphonal line, especially on the internal mould. Oblique constrictions bordered by flared ribs are present on outer and inner whorls. There are 20 umbilical bullae and about 96 ribs at 114 mm diameter.

DIMENSIONS. C.79137 – 114·0 : 49·0 (43%), 76·0 (67%), 31·0 (27%).

REMARKS. The figured specimen is very similar to Spath's paratype in ornamentation. The characteristic features of the species are its moderately inflated whorl section, well-rounded umbilical shoulder with high umbilical wall and bullate tubercles at the umbilical shoulder.

O. (*O.*) *sublaevis* Spath falls between species with greater whorl inflation like *O. globosus* Spath and *O. perinflatus* (Matheron), and those with more compressed whorls like *O. fascigerus* Spath and *O. radiatus* Spath. All these species occur at about the same stratigraphical level in the uppermost beds of the middle member of the Chichali Formation.

The species is reported for the first time from Western Kohat.

LOCALITIES. Punnu Mines and Lunda Mines in the Trans Indus Ranges, and south of Khadimakh in Western Kohat.

Olcostephanus (Olcostephanus) globosus Spath 1939

Pl. 4, fig. 1

1939 *Olcostephanus globosus* Spath : 16 ; pl. 5, figs 3a–b.
1972 *Olcostephanus* (*Olcostephanus*) *pachycyclus* Spath ; Fatmi : 320.

MATERIAL. Three specimens, C.79141–3.

HORIZON. Uppermost bed of the middle member of the Chichali Formation in the Trans Indus Ranges, and upper part of rusty brown sandstone member in Khadimakh ; Valanginian (Upper).

DESCRIPTION. The figured specimen is involute, globular and wholly septate. The whorl section is much depressed, with a broad arched venter which almost meets the nearly vertical umbilical wall at the rounded umbilical shoulder. The umbilicus is narrow. There are about 24 prominent, radially elongated, tubercles at the umbilical shoulder. From the tubercles bundles of 3 to 4 ribs pass across the venter transversely or with slight forward arching.

DIMENSIONS. C.79143 – 84·0 : 35·0 (42%), 70·0 (83%), 23·0 (25%).

REMARKS. The specimen compares favourably with Spath's holotype in side and ventral views and in the number of umbilical tubercles, but differs in its smaller number of bundled ribs per tubercle and less inflated shell. The bundles of 3 to 4 rectiradiate ribs and the whorl dimensions are closely comparable with those of *O. perinflatus* (Matheron), but *O. globosus* differs in its greater number of tubercles, less rapid increase of whorl breadth and greater size. The holotype of *O. perinflatus* (Matheron 1878 : pl. B20, figs 7a–b) is about 70 mm diameter and has a complete body chamber with a contracted macroconch-type mouth border, and 21 tubercles at the umbilical shoulder.

LOCALITIES. Chichali Pass in the Trans Indus Ranges and Khadimakh in Western Kohat.

Subgenus ***ROGERSITES*** Spath 1924

Olcostephanus (Rogersites) schenki (Oppel 1863)

Pl. 5, fig. 1

1863 *Ammonites schenki* Oppel : 286 ; pl. 81, figs 4a–c.
1903 *Holcostephanus* (*Astieria*) *schenki* (Oppel) Uhlig : 130 ; pl. XVIII, figs 2a–c.
1939 *Olcostephanus* (*Rogersites*) *schenki* (Oppel) Spath : 30 ; pl. II, fig. 6 ; pl. XVIII, figs 9–10 (with synonymy).

MATERIAL. Three specimens, C.79144–6.

HORIZON. Uppermost bed of the middle member of the Chichali Formation ; Valanginian (Upper).

DESCRIPTION. The figured specimen is involute, inflated, 70 mm in diameter, and approximately ⅓ of the outer whorl consists of body-chamber. The whorl section is depressed, the umbilicus is narrow and deep, and the umbilical wall is steep. There are about three constrictions per whorl, which are slightly more prorsiradiate than the ribs behind. The ribs on the umbilical wall are rursiradiate on the outer whorl but rectiradiate on the inner whorls, and form radially elongated tubercles on the umbilical shoulder which are sharp and conical on the inner whorl and blunt on the body-chamber. Three prorsiradiate ribs come from each tubercle and curve backwards to cross the venter radially. Occasionally ribs bifurcate higher up on the flank than the tubercles. There are 22 tubercles and 66 ribs at 70 mm diameter.

DIMENSIONS. C.79146 { 70·0 : 31·0 (44%), 42·0 (60%), 21·0 (30%).
56·0 : 25·0 (45%), 37·0 (66%), 16·0 (29%).
C.79144 – 43·0 : 19·0 (44%), 28·0 (65%), 12·0 (28%).

REMARKS. The specimens are very similar to Oppel's holotype from Tibet which was refigured and defined by Uhlig (1903). They also compare closely with Spath's figured specimen from the Trans Indus Ranges. With a complete body-chamber it is estimated that the shell reached a diameter of at least 95 to 100 mm.

LOCALITIES. Punnu Mines, Chichali Pass, Lunda Mines, Trans Indus Ranges.

Olcostephanus (Rogersites) madagascariensis Lemoine 1906

Pl. 5, figs 3, 4

1906 *Holcostephanus madagascariensis* Lemoine : 182 ; pl. 1, fig. 3.
1939 *Olcostephanus* cf. *madagascariensis* Lemoine ; Spath : 28 ; pl. XIX, fig. 3.
1962 *Olcostephanus* (*Rogersites*) *madagascariensis* Lemoine ; Collignon : pl. 82, fig. 825 (holotype refigured).

MATERIAL. Two specimens, C.79147–8.

HORIZON. Top bed of the middle member of the Chichali Formation ; Valanginian (Upper).

DESCRIPTION. C.79147 is an adult microconch with ¾ of a whorl of body chamber ending in a constricted then flared mouth border at 64 mm diameter, on which large lateral lappets are preserved. C.79148 has a slightly shorter body chamber, the mouth border not being preserved at the broken aperture at about 71 mm diameter. Both specimens have moderately evolute and inflated shells, with depressed whorl sections. Oblique constrictions followed by a flared rib are present in both. The ribs on the umbilical wall are coarse, sharp and strongly rursiradiate in C.79147 but less strong and rectiradiate in C.79148. At the umbilical shoulder they swell into sharp tubercles. Three or four rectiradiate ribs come from each tubercle and cross the venter transversely or with slight backward arching.

There are 17 umbilical ribs and tubercles and 54 ventral ribs on C.79147 and 20 and 60 respectively on C.79148.

DIMENSIONS. C.79147 – 62·0 : 29·0 (47%), 36·0 (58%), 26·0 (42%).
C.79148 – 70·0 : 26·0 (37%), 37·0 (53%), 25·0 (36%).

Remarks. These two specimens compare very closely with the holotype as well as with Spath's figured specimen. A new varietal name is proposed for C.79148, *Olcostephanus* (*Rogersites*) *madagascariensis* var. *isakhelensis* [= *O.* (*R.*) sp. nov. of Fatmi 1972 : 320] (Pl. 5, fig. 3), which is characterized by having shorter and less rursiradiate umbilical ribs and more depressed whorls.

Localities. Chichali Pass and Lunda Mines in the Trans Indus Ranges.

Family **BERRIASELLIDAE** Spath 1922

Subfamily **BERRIASELLINAE** Spath 1922

Genus ***BERRIASELLA*** Uhlig 1905

Berriasella sp. indet.

Pl. 5, fig. 2

Material. Three specimens, C.79149–51.

Horizon. Basal 3 feet (0·9 m) of middle member of the Chichali Formation; Berriasian.

Description. The figured specimen is a fragment of an evolute, septate whorl of about 120 mm diameter. The whorl section is higher than wide with subparallel flanks and narrow subtabulate or slightly sulcate venter. Shallow constrictions parallel to the rib direction are present. The ribs are weak on the umbilical wall, rectiradiate on the lower half of the flank, slightly prorsiradiate on the upper half of the flank, and terminate at the edge of a narrow mid-ventral smooth band in blunt tubercles which are more distinct on the inner whorls. On the larger whorls the ribs have a tendency to cross the venter with only slight degeneration and weakening. The ribs either bifurcate from the middle of the flank or remain simple, or rarely they bifucrate on the lower third of the flank.

Dimensions. C.79151 – 145·0 : 44·0 (30%), 37·0 (26%), 76·0 (52%).

Remarks. The species is characterized by having a very evolute shell and fairly widely spaced ribs that either bifurcate or remain simple. Its inclusion in *Berriasella* is favoured, rather than *Subthurmannia* to which it may be transitional. In the evolute shell and the presence of tubercles on the ventral margin it is comparable to *Subthurmannia* sp. indet. cf. *lorensis* (Lisson) figured by Spath (1939 : 55 ; pl. XII, figs 3a–b, 4 ; pl. XV, fig. 7) from the Trans Indus Salt Range. It differs, however, in the rib style and whorl section. The ribs on Spath's specimen are sharp and irregular. The ribs on the holotype of *S. lorensis* (Lisson) (1907 : 63, pl. IV, figs 4a–b, 5) are different : they are more or less rectiradiate, simple or bifurcating on the lower two-thirds of the flank, strongly projected forwards on the upper third of the whorl side, and conspicuously arched forwards, without degeneration, on the venter. It appears that both Spath's specimens from the Trans Indus Salt Range and the described specimen are different from *S. lorensis* (Lisson), and better-preserved material may show it to be a new species, transitional from *Berriasella* to *Subthurmannia*.

Localities. South-west of Malla Khel and Chichali Pass, Trans Indus Ranges.

Genus *SUBTHURMANNIA* Spath 1939

Subthurmannia fermori Spath 1939

Pl. 6, figs 1, 3 ; Pl. 7, fig. 1

1939 *Subthurmannia fermori* Spath : 53 ; pl. IX, figs 1, 5 ; pl. X, figs 1a–b, 7, 8.
1939 *Subthurmannia media* Spath : 50 ; pl. VIII, figs 1a–b.
1939 *Subthurmannia patella* Spath : 51 ; pl. VIII, figs 2a–b.

MATERIAL. Seven specimens, C.79152–8.

HORIZON. Basal 2 feet (0·6 m) of the middle member and uppermost bed of the lower member of the Chichali Formation ; Berriasian.

DESCRIPTION. All the specimens are wholly septate, the largest being 140 mm in diameter. The shell is evolute, with an elliptical whorl section, a rounded umbilical wall, and a venter that is tabulate or slightly sulcate on the inner whorls. Three types of ribs may be recognized which become more irregular and distant with increase of size. The commonest bifurcate from the blunt umbilical tubercles, and one of them commonly branches again at the middle of the flank. The second type remains simple, and the third bifurcates near the middle of whorl side, and normally both these types are without tubercles at the umbilical shoulder. The ribs are prorsiradiate on the flank and cross the venter with pronounced forward arching but with degeneration along the mid-siphonal line ; on the inner whorls the ribs are interrupted on the venter. At larger sizes the ribs become more irregular and include some intercalated ribs. There are about 11 umbilical tubercles and about 50 ribs per half whorl at 118 mm diameter.

DIMENSIONS. C.79152 – 118·0 : 43·0 (36%), 36·0 (31%), 43·5 (37%).
C.79154 – 91·5 : 35·0 (38%), 28·0 (31%), 29·0 (32%).
C.79155 – 124·0 : 47·5 (38%), 36·0 (29%), 42·5 (34%).
C.79157 – 102·0 : 42·0 (41%), 32·0 (31%), 32·0 (31%).

REMARKS. *Subthurmannia fermori* Spath is the type species of the genus *Subthurmannia*, established by Spath (1939) from the Trans Indus Ranges. Spath erected seven new species, all of which occur at the same stratigraphic level in the basal part of the middle member and uppermost bed of the lower member of the Chichali Formation, in a total thickness of 4 to 5 feet (c. 1⅓ m). Many of his species are transitional to each other and are so closely allied that it becomes difficult to maintain their separate identity. Those named by Spath as *S. patella* and *S. media* (C.79154–5) are very similar to *S. fermori* at similar diameters in ornamentation and other details. The minor differences such as the slightly more involute, compressed shell, less sinuous and coarser ribs of *S. media* and *S. patella* (the septate holotypes are 77 and 78 mm diameter respectively, compared with the septate holotype of *S. fermori* which is 160 mm diameter) may not be sufficient to justify a specific separation when they all occur at the same stratigraphical level. Further, the differences between *S. media* and *S. patella* are smaller still. These two are, therefore, considered here to be variants of *S. fermori*. A new variant *surgharensis* (C.79157, Pl. 7, fig. 1) is proposed, which differs from the type and other variants in being more involute, having higher whorls, a broader venter, more prominent ventral tubercles and weaker umbilical tubercles.

Subthurmannia fermori Spath is connected by various transitional fragmentary specimens in the collection with *Subthurmannia transitoria* Spath. The two, however, may be distinguished by the earlier appearance of stout, distant primary ribs and many shorter intercalatory ones in *S. transitoria*. *S. femori* also resembles *S. boissieri* (Pictet) in its large size and partly in ornamentation and whorl shape, but it is distinguished by its more rounded flank and venter at large sizes, narrower umbilicus, more pronounced forward projection of the ribs, fewer and smaller umbilical tubercles and less frequent bifurcation of the ribs on the flank.

Subthurmannia fermori and its variants are abundantly distributed in the Trans Indus Ranges and less frequently in the Samana Range in the basal part of the Cretaceous, and occupy a similar position to that of *S. boissieri* (Pictet) in Europe. The species is recorded for the first time from Western Kohat.

LOCALITIES. Many localities in the Trans Indus Salt Range, and south of Fort Lockhart in the Samana Range.

Subthurmannia filosa Spath 1939

Pl. 6, fig. 2 ; Pl. 7, fig. 3

1939 *Subthurmannia filosa* Spath : 59 ; pl. XIII, figs 5a–c.
1939 *Subthurmannia lissonioides* Spath : 52 ; pl. VIII, figs 3–4.

MATERIAL. Four specimens, C.79159–62.

HORIZON. Near the contact of the middle and lower members of the Chichali Formation ; Berriasian.

DESCRIPTION. The figured specimens are moderately involute, have an oval whorl section and the venter is rounded, subtabulate or grooved on the inner whorls. The ribs are fine and dense, prorsiradiate and curved forwards on the upper third of the flank ; they cross the venter with strong forward arching on the outer whorl but are interrupted on the inner whorl which has a smooth siphonal groove. Bifurcation of the ribs takes place near the umbilical shoulder and again at the middle of the flank.

DIMENSIONS. C.79160 – 77·0 : 30·5 (40%), 26·0 (34%), 25·0 (32%).
C.79162 – 70·0 : 29·5 (42%), 23·0 (33%), 20·0 (29%).

REMARKS. Two finely ribbed forms of *Subthurmannia* occur in the Trans Indus Range collections at the same stratigraphic level, and Spath (1939 : 52, 59) proposed the two new species *Subthurmannia filosa* and *S. lissonioides* for them. They are very closely related and *lissonioides* is considered here to be a variety of *filosa* ; with its coarser ribs it is transitional to *S. fermori* var. *media* Spath.

In its dense ribs, less forward projection of the venter and involute shell, the figured specimens resemble *Substeueroceras kooneni* (Steuer) (1897 : pl. XVII (XXXI), figs 1–4), but they differ in having bifurcation from the umbilical shoulder or the middle of the flank. In *Substeueroceras kooneni* the point of bifurcation is usually on the lower third of the flank. The resemblance, however, indicates relationship of the genera *Subthurmannia* and *Substeueroceras*. The species is reported for the first time from the Samana Range.

LOCALITIES. Chichali Pass, Makerwal, Punnu Mines in the Trans Indus Ranges and two doubtful specimens from the south of Fort Lockhart, Samana Range, Western Kohat.

Subthurmannia transitoria Spath 1939

Pl. 7, fig. 2 ; Pl. 10, fig. 4

1939 *Subthurmannia transitoria* Spath : 57 ; pl. XI, figs 1a, b.
1939 *Subthurmannia* sp. nov. aff. *transitoria* Spath : 58 ; pl. XI, figs 2, 3.

MATERIAL. Five specimens, C.79163–7.

HORIZON. Lower 2 feet (0·6 m) of the middle member and uppermost bed of the lower member of the Chichali Formation ; Berriasian.

DESCRIPTION. The shell is moderately involute, the whorl section is oval and the venter is rounded at large diameters but subtabulate, tabulate or slightly sulcate at smaller diameters. The biggest specimen is still septate at 180 mm diameter. Strong, distant primary ribs are prorsiradiate to rectiradiate on the lower half of the flank but curve forwards and divide up into 2 to 4 secondary ribs on the upper part of the flank. Some of the secondaries are intercalated. The ribs cross the venter with forward arching but are weak on the mid-venter.

DIMENSIONS. C.79163 – 180·0 : 66·0 (37%), ?51·0 (28%), ?65·0 (36%).
C.79165 – 100·0 : 43·0 (43%), 29·0 (29%), 30·0 (30%)

REMARKS. The species is easily distinguishable from *Subthurmannia fermori* Spath by its coarse distant primary ribs and more irregular secondary ribs, and the whorl section tends to be more sharply convergent towards the venter.

The new variant *S. transitoria* var. *noori* (C.79165, Pl. 10, fig. 4) is similar to Spath's more involute form figured doubtfully as *S. transitoria* (1939 : pl. XI, figs 2, 3). It is more involute and has a more elevated whorl section than the holotype. *Subthurmannia transitoria* is a very commonly distributed species along with *S. fermori* in the Trans Indus Ranges.

LOCALITIES. Many localities of the Trans Indus Ranges.

Subthurmannia sp. indet.

1972 *Subthurmannia* aff. *boissieri* (Pictet) ; Fatmi : 320.
1972 *Subthurmannia* aff. *pseudopunctata* Spath ; Fatmi : 320.

MATERIAL. Nine fragments, C.79168–76.

HORIZON. Lower part of the middle member and upper part of the lower member of the Chichali Formation ; Berriasian.

REMARKS. There are several fragmentary specimens of the genus *Subthurmannia* which are difficult to assign to any one species due to their poor preservation. Most probably belong to *S. fermori*, *S. transitoria* or *S. filosa*, but one of them from the

Samana Range has some resemblance to *S. boissieri* Pictet. The specimens C.79175–6 resemble *Subthurmannia* (gen. nov. ?) *pseudopunctata* Spath (1939 : 61 ; pl. XIV, figs 6a–c).

LOCALITIES. Several localities in the Trans Indus Ranges and south of Fort Lockhart, Samana Range.

Genus ***PROTACANTHODISCUS*** Spath 1923

Protacanthodiscus asiaticus (Uhlig 1910)

Pl. 8, fig. 6

1910 *Hoplites* (*Acanthodiscus*) *asiaticus* Uhlig : 225 ; pl. XXIV, figs 1a–b.

MATERIAL. One specimen, C.79178.

HORIZON. Near the contact of the middle and lower members of the Chichali Formation ; Berriasian.

DESCRIPTION. The specimen is rather evolute, septate to 120 mm diameter and the whorl section is higher than wide with a fairly broad tabulate venter. The ribs start in pairs at tubercles on the umbilical shoulder and bifurcate at tubercles in the middle of the flank. Some ribs are intercalated from about the lower or middle part of the flank, and a few ribs remain simple. There are three rows of tubercles. The tubercles near the umbilical shoulder are located on stout primary ribs from which the branching takes place. The mid-lateral row is more distantly and irregularly distributed and most ribs branch again at this row of tubercles. The small, sharp, oblique tubercles of the third row are located on each rib near the ventral margin. The ribs bend forwards on approaching the ventral margin and are much reduced on the tabulate venter.

DIMENSIONS. C.79178 – 120·0 : 47·0 (39%), ?35·0 (29%), 43·0 (36%).

REMARKS. The specimen matches Uhlig's holotype from Spiti in dimensions and ornamentation except that Uhlig's figure shows a smoother mid-ventral area. It occurs in association with *Subthurmannia*, and in whorl shape, ribbing and size it compares well with *S. fermori*, but the presence of prominent umbilical and mid-lateral tubercles and a broad tabulate venter suggests its inclusion in the genus *Protacanthodiscus*, which has similar features though the whorl section is less elevated. *Protacanthodiscus* is said to occur only in the Tithonian (Arkell *et al.* 1957 : L352) but it is interesting to note that Mazenot (1939) figured a few forms of *Berriasella* (*B. malbosi*, *B. jabronensis* and *B. isaria*) from the Berriasian, and *B. chaperi* and *B. adpera* from the Upper Tithonian of France, which appear to be better placed in *Protacanthodiscus*. The type species of *Berriasella*, *B. privasensis* (Pictet), does not have tubercles on the middle of the flank and umbilical shoulder. Similarly the type species of *Subthurmannia*, *S. fermori* Spath (1939 : pl. IX, fig. 1), does not have the mid-lateral tubercles and has a narrower venter. *Subthurmannia* is considered to be a Berriasian genus, and the occurrence of *P. asiaticus* at the same level suggests that *Protacanthodiscus* may extend up into the Berriasian.

LOCALITY. Chichali Pass, Trans Indus Ranges.

Protacanthodiscus sp. indet.

Material. One fragment, C.79177.

Horizon. About 3 feet (c. 1 m) below the base of the middle member of Chichali Formation ; Berriasian.

Remarks. The specimen is poorly preserved and is recorded mainly because of its stratigraphic importance. It occurs just near the base of the *Subthurmannia* beds. It differs from most of the *Subthurmannia* species of the area in having small, prominent, sharp ventral tubercles and occasional mid-lateral and umbilical tubercles. The ribbing, however, differs little from the genus *Subthurmannia.*

In side view and ornamentation it is comparable with *Berriasella parahimouna* Mazenot (1939 : 92 ; pl. XII, figs 2a–b), but differs in having a wider whorl section. It also resembles *Protacanthodiscus andreai* (Kilian) (Mazenot 1939 : pl. XII, figs 1a–b) but differs in details of ornamentation.

Mazenot assigned a Berriasian age to *B. parahimouna,* whose generic affinities appear to be closer to *Protacanthodiscus* than to *Berriasella* as it shows irregular lateral and umbilical tubercles, a feature typical of *Protacanthodiscus.*

Locality. Lunda Mines, Trans Indus Ranges.

Subfamily **NEOCOMITINAE** Spath 1924

Genus ***THURMANNICERAS*** Cossmann 1901

Thurmanniceras sp. indet. 1

Pl. 10, fig. 1

Material. Three fragments, C.79179–81.

Horizon. 4 feet (1·22 m) above the base of the middle member of the Chichali Formation ; Valanginian (Lower).

Description. The specimen consists of a septate fragment which has a whorl height of 46 mm and whorl breadth of 40 mm. The whorl section is subrectangular with flattened flanks and a broad, tabulate, and slightly sulcate venter. The ribs are slightly sinuous, prorsiradiate and weak near the middle of the flank. Some of the ribs bifurcate from the umbilical bullae and occasionally branch again at the middle of the flank. In addition there are ribs which bifurcate at the middle of the flank only, or are intercalated and start at the middle of the flank. All the ribs are strong on the ventral–lateral shoulder, where they swell into small transversely elongated tubercles, but they are weakened or interrupted on the mid-ventral area. Shallow constrictions parallel to the rib direction are present.

Remarks. Spath (1939 : 81 ; pl. X, fig. 6) figured the ventral view of a specimen from the Trans Indus Salt Range and doubtfully assigned it to *Thurmannites* (?) sp. indet. cf. *pronecostatus* (Felix). The present specimen is similar but has more flattened flanks and a broader venter. In its broad flat venter it compares with *T. umbilicocostatum* (Collignon 1962 : 195 ; fig. 894) but differs in having fewer and more prominent umbilical tubercles. The suture line is complex and is comparable with that of *Hoplites* (*Neocomites*) *scientychus* Uhlig (1902 : pl. 5, fig. 1a) which probably belongs to *Thurmanniceras* rather than *Neocomites*.

Locality. South-west of Malla Khel, Trans Indus Ranges.

Thurmanniceras sp. indet. 2

Material. Four fragments, C.79182–5.

Horizon. 5 to 6 feet (c. $1\frac{2}{3}$ m) above the base of the middle member of the Chichali Formation ; Valanginian (Lower).

Remarks. The largest fragment is septate and has a whorl height of 50 mm and a whorl breadth of 34 mm. The whorl section is subrectangular, much higher than wide, with nearly flat flanks and a tabulate or slightly rounded venter.

The species is more compressed than *Thurmanniceras* sp. indet. 1, above. It resembles Spath's (1939 : 87 ; pl. XXII, figs 11a–b) *Neocomites* aff. *neocomiensiformis* (Uhlig), from the Trans Indus Salt Range, in ventral view. It is characterized by its large size (as is also *N.* aff. *neocomiensiformis*), compressed whorls, rather weak ribs and oblique blunt tubercles (similar to *Kilianella*) on the ventral shoulder. Incorporating characters of *Neocomites*, *Thurmanniceras* and *Kilianella* it appears to be a transitional form.

Localities. Chichali Pass, Trans Indus Ranges and south of Fort Lockhart, Samana Range, Western Kohat.

Genus ***NEOCOMITES*** Uhlig 1905

Subgenus ***NEOCOMITES*** Uhlig 1905

Neocomites (Neocomites) copei sp. nov.

Pl. 8, fig. 1

Holotype. C.79186, the only specimen.

Horizon. 7 feet (2·13 m) below the top of the middle member of the Chichali Formation ; Valanginian (Lower).

Diagnosis. Involute, compressed, whorl section, subrectangular with gently arched flanks and tabulate to slightly sulcate venter ; umbilicus very narrow, with vertical umbilical wall and angled umbilical shoulder ; 3 or 4 shallow constrictions, 32 primary ribs and 14 umbilical tubercles at 55 mm diameter.

Description. The specimen is 55 mm in diameter and septate, though the beginning of the body-chamber may be present. The whorl section is compressed and much higher than wide. The flanks are arched and converge towards a narrow tabulate or very gently sulcate venter.

The ribs are prominent on the inner whorl but become weaker on the outer whorl ; they are sinuous, prorsiradiate, and projected forwards on the upper third of the flank, and they usually bifurcate on the middle or upper part of the flank. There are small tubercles at the umbilical shoulder from which the ribs start in pairs, and another row of small tubercles at the ventral termination of all the ribs. The mid-ventral area is smooth. There are shallow sinuous constructions parallel to the rib direction.

DIMENSIONS. C.79186–55·5 : 29·0 (52%), 16·5 (30%), 9·0 (16%).

REMARKS. The species resembles *Neocomites* (*N.*) *neocomiensis* var. *subtenuis* Sayn (1907 : 30 ; pl. 5, fig. 5) but differs in having stronger umbilical tubercles. It may also be compared with *N.* (*N.*) *paraplesius* (Uhlig 1902 : 59 ; pl. 11, fig. 8) but differs in being more compressed and in having stronger umbilical tubercles.

LOCALITY. South-west of Malla Khel, Trans Indus Ranges.

Neocomites (Neocomites) sp. indet.

1972 *Neocomites* (*Calliptychoceras*) spp. nov. Fatmi : 319.

MATERIAL. Three fragments, C.79187–9.

HORIZON. 6 to 7 feet (c. 2 m) below the top of middle member of Chichali Formation ; Valanginian (Lower).

REMARKS. The fragments are poorly preserved and may belong to more than one species of *Neocomites*. The ribbing and whorl section suggest affinities with *N.* (*N.*) *teschenensis* (Uhlig), *N.* (*N.*) *campylotoxus* (Uhlig) or *N.* (*N.*) *copei* sp. nov.

LOCALITIES. Chichali Pass, Lunda Mines, north of Kalabagh, Trans Indus Ranges.

Neocomites (Neocomites) campylotoxus (Uhlig 1902)

Pl. 8, figs 3, 4

1902 *Hoplites campylotoxus* Uhlig : 49 ; pl. 4, figs 1–3.
1972 *Kilianella* sp. nov. Fatmi : 319–20, 362.

MATERIAL. Three specimens, C.79190–2.

HORIZON. 6 feet (1·83 m) below the top of middle member of Chichali Formation in the Trans Indus Ranges and middle part of rusty brown sandstone member at Khadimakh ; Valanginian (Lower).

DESCRIPTION. The figured specimen is moderately evolute, compressed and about 55 mm in diameter. The last septum occurs at a diameter of 45 mm. The whorl section is elliptical with arched flanks and a narrow tabulate–sulcate venter. The ribs are sinuous on the outer whorl but straighter on the inner whorls. Most of them are single and only occasional ribs bifurcate at the middle of the flank. They swell near the ventral shoulder into oblique tubercles and the mid-ventral area appears to be smooth.

DIMENSIONS. C.79191 – 45·0 : 18·0 (40%), ?11·0 (24%), 15·5 (34%).

REMARKS. The figured specimen compares closely with Uhlig's holotype. In ribbing and tuberculation it is also comparable with *Kilianella pexiptycha* (Uhlig) and *K. leptosma* (Uhlig), but differs in being less evolute and lacking constrictions.

The specimen C.79192 is more evolute and has a less elevated whorl section but the ribbing style is very similar.

LOCALITIES. Samana Range, Khadimakh in Western Kohat and Chichali Pass in the Trans Indus Ranges.

Neocomites (Neocomites) pycnoptychus (Uhlig 1910)

Pl. 8, fig. 2

1910 *Hoplites (Neocomites) pycnoptychus* Uhlig : 252 ; pl. LXXXVII, figs 1a–c.

MATERIAL. Three specimens, C.79193–5.

HORIZON. 6 to 7 feet (c. 2 m) below the top of middle member of the Chichali Formation ; Valanginian (Lower).

DESCRIPTION. The figured specimen is wholly septate, the whorl section is subrectangular, higher than wide, the flanks are gently arched and converge towards a fairly broad, tabulate to slightly sulcate venter. The ribs are sinuous and prorsiradiate ; they swell into tubercles at the umbilical shoulder and show slight swelling into incipient tubercles at the ventral shoulder. Ribs commonly bifurcate from the umbilical tubercles and one or both ribs branch again near the middle of the flank. All the ribs are interrupted on the slightly sulcate, smooth venter.

DIMENSIONS. C.79193 – 63·0 : 26·0 (41%), 21·0 (33%), 20·5 (33%).

REMARKS. The figured specimen is similar to Uhlig's original specimen from Lochambelkichak, Spiti area. Uhlig's specimen shows the beginning of the body-chamber at the aperture at 56·5 mm diameter. The species is recorded for the first time from the Trans Indus Ranges.

LOCALITIES. South-west of Malla Khel, and one doubtful specimen from Makerwal, Trans Indus Ranges.

Neocomites (Neocomites) similis Spath 1939

Pl. 8, figs 5, 7 ; Pl. 9, figs 1, 3

1939 *Neocomites similis* Spath : 83 ; pl. XI, figs 5a–b.
1972 *Neocomites (Odontodiscoceras) similis* Spath ; Fatmi : 319.

MATERIAL. Ten specimens, C.79196–205.

HORIZON. 4 to 5 feet (c. 1½ m) below the top of the middle member of the Chichali Formation ; Valanginian (Lower).

DESCRIPTION. The shell is involute, compressed on the inner whorls but more inflated on the body-chamber. The whorl section is tall and compressed, with an inclined umbilical wall and a tabulate venter. On the body-chamber the middle of the venter tends to be raised. The ornament consists of primary, secondary and intercalated ribs which are prorsiradiate and sinuous on the flanks and are more strongly projected forwards on approaching the venter. They swell into oblique tubercles at the edge of the venter and form weak, forwardly-directed chevrons on the venter, especially on the body-chamber, but are interrupted along the mid-ventral line. There are moderately strong tubercles at the umbilical shoulder. The ribs bifurcate and trifurcate irregularly on the lower half of the flank. Some ribs remain simple and many secondary ribs are intercalated at the middle of the flank. There are 21 primary ribs with umbilical tubercles at 56 mm diameter and 24 at 36 mm diameter. The rib density increases on the inner whorls.

DIMENSIONS. C.79196 – 56·0 : 26·5 (47%), 17·0 (30%), 12·5 (22%).
C.79197 – 36·0 : 17·0 (47%), 11·0 (31%), 8·0 (22%).
C.79198 – 43·0 : 20·0 (47%), 13·0 (30%), 10·0 (23%).
C.79203 – 77·0 : 33·0 (44%), ? 19·0 (24%).

REMARKS. The figured specimens are similar to Spath's holotype but are more complete and better preserved. One of them (C.79197) shows part of the body-chamber with strong ribbing and tuberculation and a more inflated whorl section. In whorl section and amount of involution of the inner septate whorls the species is comparable with *Neocomites neocomiensis* (d'Orbigny), but differs in ornament details and in having an inclined rather than vertical umbilical wall. *N. neocomiensis* (d'Orbigny) has sheaves of 4 ribs from the umbilical tubercles, while in *N. similis* (Spath) the ribs branch more commonly from the lower half of the flank rather than from the umbilical tubercles, and they are more strongly projected.

The species is much more closely comparable with *Neocomites* (? *Odontodiscoceras*) *montanus* (Uhlig) and *N.* (? *O.*) *indomontanus* (Uhlig 1910 : 249 ; pl. XC, figs 1, 3, 5, 7) in ornament, whorl section and size, but differs in having stronger prorsiradiate ribs, somewhat different rib bifurcation on the inner whorls and less prominent umbilical and ventral tubercles.

Spath (1939 : 91) favoured the inclusion of *N. montanus* in the subgenus *Odontodiscoceras*, and indeed the ribs (and those of *N. similis* Spath) show stronger resemblance on outer whorls to those of the subgenus *Odontodiscoceras* rather than the true *Neocomites*. The inner whorls, however, are closer to *Neocomites*. The clavi-like tubercles on the ventral shoulder and the forward extension of ribs on the venter as weak chevrons, especially on the body-chamber, are characters of *Lyticoceras*. *Neocomites similis* Spath and *N. montanus* (Uhlig) might be intermediate forms which connect *Neocomites* with *Odontodiscoceras* and *Lyticoceras*. The *Lyticoceras* venter and *Odontodiscoceras* ribbing appear on the outer whorl, while the inner whorls are more like true *Neocomites*.

LOCALITIES. Chichali Pass, Trans Indus Ranges.

Neocomites (Neocomites) trezanensis Sayn 1907

Pl. 9, fig. 4

1907 *Neocomites trezanensis* Sayn : 34 ; pl. 3, figs 20, 25 ; pl. 4, fig. 5.

MATERIAL. Two specimens, C.79206–7.

HORIZON. 5 feet (1½ m) below the top of the middle member of the Chichali Formation ; Valanginian (Lower).

Description. The figured specimen is septate to 40 mm diameter, then has a short fragment of body-chamber. The whorl section is higher than wide, and the flanks converge towards a sulcate venter. There are 6 to 7 moderately deep sinuous constrictions per whorl running parallel to the rib direction. The ribs are strong, prorsiradiate and slightly sinuous, and many bifurcate from prominent umbilical tubercles and branch again on the middle of the flank. Some ribs are without tubercles at the umbilical shoulder and either bifurcate on the middle of the flank or remain simple. All the ribs terminate at the ventral shoulder in sharp oblique tubercles and the venter is smooth and sulcate.

Dimensions. C.79206 – 40·0 : 17·5 (44%), ?14·0 (35%), 12·0 (30%).

Remarks. The figured specimen is very similar to Sayn's holotype except that in the holotype the constrictions are less prominent. It may be compared to *N.* (*Calliptychoceras*) *calliptychus* (Uhlig 1910 : 251 ; pl. LXXXVII, figs 2a–c) from Lochambelkichak, Spiti, in ornament and whorl section but differs in its smaller size, steeper umbilical wall, prominent and frequent constrictions bordered by thick blunt ventral clavi, fewer umbilical tubercles and less sinuous, forwardly-projected ribs on the flank.

Localities. Punnu Mines, north of Kalabagh, Trans Indus Ranges.

Subgenus ***PARANDICERAS*** Spath 1939

Neocomites (Parandiceras) rota (Spath 1939)

Pl. 9, figs 2, 5

1939 *Parandiceras rota* Spath : 77 ; pl. XV, figs 1a–b.
1972 *Neocomites* (*Parandiceras*) *theodorii* (Oppel) ; Fatmi : 319, 362.
1972 *Neocomites* (*Parandiceras*) aff. *indicus* (Uhlig) ; Fatmi : 319.

Material. Six specimens, C.79208–13.

Horizon. 4 to 5 feet (c. 1½ m) below the top of the middle member of the Chichali Formation ; Valanginian (Lower).

Description. The shell is moderately evolute. The whorl section is higher than wide, wedge-shaped on the outer whorls but more compressed on inner whorls, and converges towards a narrow, tabulate or sulcate venter. There are shallow constrictions parallel to the ribs. The ribs are straight and prorsiradiate on the flanks, and commonly bifurcate on the middle or lower part of the flank. There are occasional simple ribs and some which bifurcate at the umbilical shoulder, especially on the inner whorls. The ribs swell into small tubercles on the umbilical shoulder and end in prominent tubercles at the edge of the venter, which are oblique and extend onto the sides of the venter.

Dimensions. C.79208 – 48·0 : 21·0 (44%), 15·0 (31%), 12·0 (5%).

Remarks. Spath's genus *Parandiceras* (with type species *Parandiceras rota* Spath) is considered to be a subgenus of *Neocomites* because (1) *Parandiceras* occurs in the Lower Valanginian alongside typical *Neocomites*, (2) the inner whorls of *Parandiceras* show frequent bifurcation from the umbilical shoulder like that of

Neocomites, and (3) *P. rota* is connected with *Neocomites* through intermediate forms like *Neocomites theodorii* (Oppel) (Uhlig 1910 : 260 ; pl. LXXXIX, figs 1a–d, 2a–b) and *N. indicus* (Uhlig), which have simple and bifurcating ribs on the outer whorl but have more double bifurcating ribs, of the *Neocomites* type, on the inner whorls, and a more involute shell. The umbilical tubercles are small, like *Neocomites*, but the ventral tubercles are strong, as in *Calliptychoceras*. The venter is narrower and the ventral shoulder more angular than in *Calliptychoceras* and *Odontodiscoceras*.

It is probable that several offshoots of *Neocomites* appeared during the Lower Valanginian. The *Odontodiscoceras* trend is marked by greater inflation of the whorl, a wider umbilicus, stronger umbilical and ventral tubercles, and bifurcation and trifurcation of the ribs on the flank. In the *Parandiceras* trend the shell becomes more evolute and less compressed, the venter becomes narrower, the ribs mainly bifurcate at the middle of the flank and there are some intercalated ribs. The umbilical tubercles become weaker and the ventral tubercles stronger. In the *Calliptychoceras* trend the shell is more evolute, the whorl section more inflated, the umbilical and ventral tubercles are stronger and the sulcate venter is moderately broad. *Neocomites* itself persisted from the Berriasian to the Valanginian and is characterized by its compressed, involute shell, subrectangular whorl section, narrow umbilicus, small umbilical and ventral tubercles, and branching of the ribs from the umbilical tubercles shoulder and branching again at the middle of the flank.

It appears that during the Lower Valanginian large species of *Neocomites* appeared, with coarser, sinuous ribs (*N. teschenensis*, *N. platycostatus* and *N. neocomensiformis*), and with a more evolute shell and greater projection of the ribs on the venter they gave rise to the genus *Lyticoceras* during Upper Valanginian times. The very interesting species described here, *N.* (*N.*) *similis* Spath (p. 280), shows typical *Neocomites* ribbing and whorl shape on the inner whorls and *Odontodiscoceras* ribbing and whorl shape on the outer whorl. It has a tendency to oblique tuberculation and forward projection of the ribs on the venter of the outer whorl like that of *Lyticoceras*, which occurs at a higher level in the Upper Valanginian *Olcostephanus* and *Rogersites* beds of the Trans Indus Ranges.

It is concluded, therefore, that *Calliptychoceras*, *Odontodiscoceras* and *Parandiceras* may best be regarded as subgenera of *Neocomites* on the basis of their similar stratigraphic position in the Lower Valanginian and some common characteristics suggesting a close ancestry.

LOCALITIES. South-west of Malla Khel, Chichali Pass, in the Trans Indus Ranges.

Genus ***LYTICOCERAS*** Hyatt 1900

Subgenus ***BESAIRIECERAS*** Collignon 1962

Lyticoceras (Besairieceras) colcanapi (Collignon 1962)

Pl. 9, fig. 6 ; Pl. 10, fig. 3

1962 *Besairieceras colcanapi* Collignon : 58 ; pl. 196, fig. 899 ; pl. 197, fig. 900.

MATERIAL. Six specimens, C.79214–9.

HORIZON. Upper part of the middle member of the Chichali Formation; Valanginian (Upper).

DESCRIPTION. One of the figured specimens (Pl. 10, fig. 3) is 95 mm in diameter and has nearly a quarter whorl of body-chamber, while the other (Pl. 9, fig. 6) has nearly half a whorl of body-chamber. The whorls are evolute, the whorl section is subrectangular and the venter is subtabulate on the outer whorls but sulcate on the inner whorls. Fairly deep constrictions on the inner whorls become shallow, then disappear on the outer whorl. The ribs are slightly sinuous and prorsiradiate but are more strongly projected forwards near the ventral shoulder where they swell into weak tubercles. Ribs bifurcate from the umbilical shoulder, and sometimes again in the middle of the flank. The ribs form forwardly-directed chevrons on the venter, and border a mid-ventral smooth band on the outer whorl and a sulcus on the inner whorls. Umbilical tubercles appear at about 50 mm diameter and become prominent and sharp at larger sizes.

DIMENSIONS. C.79214 – 95·0 : 39·0 (41%), 27·0 (28%), 35·0 (37%).
C.79216 – 66·0 : 24·0 (36%), 20·0 (30%), 24·0 (36%).

REMARKS. One of the figured specimens (Pl. 10, fig. 3) is very similar to Collignon's holotype from the Upper Valanginian of Madagascar. In Pakistan the genus occurs in the *Olcostephanus* and *Rogersites* beds, also of Upper Valanginian age. Collignon created the genus *Besairieceras* for ammonites which develop large inwardly-pointing tubercles on the umbilical edge but are otherwise very similar to *Lyticoceras*. These Pakistan specimens show the commencement of the umbilical tubercles and are referred, therefore, to *Besairieceras*, which is considered here to be a subgenus of *Lyticoceras*. The fragmentary specimen from the Trans Indus Salt Range described by Spath (1939 : 90; pl. XVIII, figs 5a–b) as *N.* (? *Lyticoceras*) sp. nov. is very similar but has stronger forwards projection of the ribs of the venter, and is rather more involute.

LOCALITIES. Malla Khel, Lunda Mines, Trans Indus Ranges, and upper part of rusty brown sandstone member in Khadimakh, Western Kohat.

Lyticoceras (Besairieceras) planecostatum (Collignon 1962)

Pl. 10, fig. 5

1962 *Besairieceras planecostatum* Collignon : pl. 198, fig. 903.

MATERIAL. Two specimens, C.79220–1.

HORIZON. Upper part of middle member of the Chichali Formation; Valanginian (Upper).

DESCRIPTION. The figured specimen is part of a body-chamber with a whorl height of 39 mm and a whorl breadth of 25 mm. The whorl section is rectangular, with flat flanks and a fairly broad tabulate venter. The ribs are prorsiradiate, strongly sinuous and forwardly projected at the ventral shoulder. They cross the venter with much weakening along the slightly raised mid-ventral line. The ribs commonly bifurcate from blunt umbilical tubercles, and occasionally bifurcate again about the middle of the flank. The ribs swell into oblique tubercles at the ventral shoulder.

REMARKS. The species differs from *Lyticoceras* (*B.*) *colcanapi* (Collignon) in its strongly sinuous ribs, its larger swelling at the edge of the venter and the larger chevrons on the venter.

LOCALITIES. South of Fort Lockhart, Samana Range, Western Kohat and Punnu Mines, Chichali Pass, Malla Khel, Trans Indus Ranges.

Genus ***NEOCOSMOCERAS*** Blanchet 1922

Neocosmoceras octagonum (Blanford 1864)

Pl. 10, fig. 2

1864 *Ammonites octagonus* (Strachey MS) Blanford : 128 ; pl. 1, figs 5a–c.
1910 *Hoplites* (*Acanthodiscus*) *octagonus* (Strachey) ; Uhlig : 204 ; pl. XXII, figs 1a–c ; pl. XIX, figs 1a–b ; pl. XX, figs 1a–b, 2 ; pl. XXVI, figs 3a–c (with synonymy).
1939 *Neocosmoceras octagonum* (Strachey MS) Blanford sp. ; Spath : 71.

MATERIAL. Two specimens, C.79222–3.

HORIZON. Upper part of the lower member of the Chichali Formation ; Berriasian.

DESCRIPTION. Both specimens are fragments ; the larger one is part of a shell about 100 mm in diameter. The whorl section is octagonal and the venter is slightly sulcate. The ornament consists of coarse, distant ribs which are prorsiradiate on the flank and mainly simple, but occasionally bifurcate. They are surmounted by umbilical, lateral and ventrolateral tubercles, of which the latter are the most prominently elevated and bullate. The umbilical tubercles are weak and are occasionally represented only by a rib swelling. The ribs do not cross the smooth, slightly sulcate venter.

REMARKS. The figured specimen is very similar in ornament and whorl shape to Uhlig's figure of *N. octagonum* from the Upper and Middle Spiti shales. Blanford's (1864) original figured specimen, however, has a body-chamber at a much smaller size, and is fragmentary. The present specimen differs in having weaker umbilical tubercles and a slightly broader venter, and may constitute a variety. It is also closely comparable with *N. octagonoides* (Uhlig 1910 : pl. XXVII, figs 1a–b, 2a–b) which, in fact, is very similar to *N. octagonum*. Among the European species, it is fairly close to *N. rerollei* (Paquier 1900 : pl. VII, fig. 3) and its subspecies *lamberti* Kilian as figured in Mazenot (1939 : pl. XXIX, figs 5–6). It differs, however, in having a wider whorl section.

In the Samana Range, the species occurs just below the *Subthurmannia* bed, near the Jurassic/Cretaceous boundary.

LOCALITY. South of Fort Lockhart, Samana Range, Western Kohat.

Neocosmoceras sp. indet.

MATERIAL. One fragment, C.79224.

HORIZON. Basal part of the middle member of the Chichali Formation ; Berriasian.

REMARKS. This is a poorly preserved, wholly septate, quarter whorl fragment at about 150 mm shell diameter, which shows considerable resemblance to the holotype of *Neocosmoceras spitiensis* (Uhlig 1910 : 221 ; pl. XXVI, figs 2a–c) from Lochambelkichak, Spiti. However, it is rather more evolute and has a narrower venter than Uhlig's specimen.

LOCALITY. Punnu Mines, Trans Indus Ranges.

? *Neocosmoceras subradiatum* (Uhlig)

Pl. 10, fig. 6

1910 *Hoplites* (*Acanthodiscus*) *subradiatus* Uhlig : 208 ; pl. XXIII, figs 1a–b ; pl. XXVI, fig. 1.
1933 *Octagoniceras subradiatus* (Uhlig) ; Spath : 804.

MATERIAL. Three fragments, C.79225–7.

HORIZON. Near the contact of the lower and middle members of the Chichali Formation, in the Trans Indus Ranges, and 5 feet ($1\frac{1}{2}$ m) above the base of the Chichali Formation at Kala Chitta ; Berriasian.

DESCRIPTION. The three fragmentary specimens display evolute octagonal whorls in which the whorl breadth exceeds the whorl height. The primary ribs are hardly more than swellings between the large umbilical and lateral bullae. Secondary ribs extend from the lateral bullae to the ventral shoulder and onto the side of the venter. At the ventral shoulder they are raised into oblique tubercles. The ribs on the side of the venter are inclined slightly forwards and are interrupted along the siphonal line.

REMARKS. These fragments are similar to Uhlig's holotype from the Spiti area. The weak ventral tubercles and extension of the ribs onto the venter are features not usually found in *Neocosmoceras*, and perhaps the species may constitute a new subgenus. It is possible that *Neocosmoceras* evolved from the Tithonian genus *Protacanthodiscus*, which gave rise to two distinct forms : the true *Neocosmoceras* (*N. sayni*) developed strong ventral clavi, while in *N. subradiatum* ventral clavi or tubercles are weak or absent.

LOCALITIES. Punnu Mines, Trans Indus Ranges and west of Ghoramar, Kala Chitta Range.

Genus ***KILIANELLA*** Uhlig 1905

Kilianella asiatica Spath 1939

Pl. 11, figs 1, 5

1910 *Hoplites* (*Kilianella*) *pexiptychus* Uhlig : 229 ; pl. LXXXII, figs 2a–c.
1939 *Kilianella asiatica* Spath : 93 ; pl. XIV, figs 2a–b.

Material. Five specimens, C.79228–32.

Horizon. 4 to 6 feet (1·2–1·8 m) below the top of the middle member of the Chichali Formation ; Valanginian (Lower).

Description. The whorls are evolute, the whorl section is subquadrate, higher than wide, and the venter is tabulate and has a mid-ventral sulcus. The ribs are strong, sharp and sinuous, and are projected well forwards at the ventral shoulder and on the sides of the venter but are interrupted at the smooth, narrow mid-venter. Some ribs bifurcate from the umbilical shoulder and again at the middle of the flank, and occasional ribs are simple. The bifurcation point on the middle of the flank is sometimes raised into small tubercles which are distinct on the outer whorl but are less prominent on the inner whorls. The ribs are also slightly swollen at the ventrolateral edge.

Dimensions. C.79228 – 42·0 : 16·7 (40%), 15·0 (36%), 15·5 (37%).

Remarks. The specimen described from the Spiti area as *K. pexiptycha* (Uhlig 1910 : pl. LXXXII, figs 2a–c) closely resembles *K. asiatica* and differs significantly from the true *K. pexiptycha* (Uhlig), as was pointed out by Spath (1939 : 94). Both the Spiti and Trans Indus specimens of *Kilianella asiatica* differ from the original of *K. pexiptycha* in having very sinuous, sharp ribs, no constrictions, a more inflated whorl section, more simple ribs and less prominent ventral clavi. Uhlig (1910 : 229) pointed out the indistinct nature or absence of constrictions and greater sinuosity of the ribs of his Spiti specimen but considered it to belong to *K. pexiptycha* because a great deal of variation existed in this group. Uhlig's Spiti specimen has more pronounced ventral swellings and less sinuous ribs than the Trans Indus specimens but it appears to be closer to *K. asiatica* than to *K. pexiptycha* which has denser ribs.

Locality. Chichali Pass, Punnu Mines, Trans Indus Ranges.

***Kilianella* cf. *besairiei* Spath 1939**

Pl. 11, fig. 3

1939 *Kilianella besairiei* Spath : 26 ; pl. XVI, figs 4a–b, 5a–c.

Material. Two specimens, C.79233–4.

Horizon. About 7 feet (2 m) below the top of the middle member of Chichali Formation ; Valanginian (Lower).

Description. The figured specimen is a fragment of a body-chamber, with a quadrilateral whorl section which narrows to a fairly broad venter that is sulcate due to thick bordering clavi. The ribs are coarse, strongly sinuous, both simple and bifurcating, and they swell into thick blunt oblique tubercles on the ventral shoulder and are interrupted along the middle of the venter.

Remarks. These specimens strongly resemble the body-chamber fragment figured by Spath (1939 : pl. XVI, figs 5a–c) from the Lower Neocomian of Madagascar but differ in having more frequent bifurcation from the middle of the flank.

Locality. Chichali Pass, Trans Indus Ranges.

Genus ***DISTOLOCERAS*** Hyatt 1900

Distoloceras sp. indet.

Pl. 11, fig. 2

Material. One specimen, C.79235.

Horizon. 6 feet (1·83 m) below the top of the middle member of the Chichali Formation; Valanginian (Lower).

Description. This specimen is evolute, wholly septate and 61 mm in diameter. The whorl section is compressed, elliptical with a narrow tabulate venter and a rounded umbilical edge. The ribs are prorsiradiate on the flank and curve strongly forwards near the venter. They are mainly single but some bifurcate from the umbilical shoulder or in the middle of the flank. On the outer whorl there are some intercalated ribs. On the venter the ribs are weaker, and they are interrupted at the mid-venter. Fairly strong tubercles occur on every second or third rib just ventral of the mid-lateral joint and also at the edge of the venter. The ribs in between are either non-tuberculate or bear much smaller lateral and ventral tubercles.

Dimensions. C.79235 – 61·0: 25·5 (42%), 20·0 (33%), 21·0 (34%).

Remarks. This specimen is too small to show the uncoiling stage exhibited by some species of *Distoloceras*. Its morphological characters agree with that genus, though the ribs are somewhat finer and the tubercles smaller than in either *D. hystrix* (Phillips) or *D. pavlovi* Spath (Wright 1957: 360, figs 472, 473). Its Lower Valanginian age in Pakistan may indicate that it is transitional between *Neocomites* or *Kilianella* and the true *Distoloceras*, which occurs mainly in the Lower Hauterivian.

Locality. South-west of Malla Khel, Trans Indus Ranges.

Distoloceras sp. indet.

Pl. 11, fig. 4

Material. Two fragments, C.79236–7.

Horizon. Upper 2 feet (0·61 m) of the middle member of the Chichali Formation; Valanginian (Upper).

Remarks. These two fragments do not differ in any respect from similar-sized parts of the more complete Lower Valanginian specimen of Pl. 11, fig. 2. They do not, therefore, require separate description. Both of them are fragments of immature body-chambers of 45 to 50 mm diameter. They probably represent an early species of *Distoloceras*.

Localities. South-west of Malla Khel and Lunda Mines, Trans Indus Ranges.

Genus ***SARASINELLA*** Uhlig 1905

Sarasinella uhligi Spath 1939

Pl. 12, fig. 2

1939 *Sarasinella uhligi* Spath: 99; pl. XII, fig. 5; pl. XIV, figs 1a, b; pl. XXI, figs 5a–b, 6.

MATERIAL. Three specimens, C.79238–40.

HORIZON. 8 feet (2·4 m) below the top of the middle member of the Chichali Formation ; Valanginian (Lower).

DESCRIPTION. All the specimens are septate fragments of fairly involute, moderately compressed whorls, with quadrate whorl sections, in which the flat flanks are convergent towards a fairly broad, tabulate or slightly sulcate venter. The ribs are moderately dense and rectiradiate and curve slightly forwards near the venter. They bifurcate from the umbilical tubercles and again in the middle of the flank, and they pass onto the sides of the venter but are interrupted in the middle. There are a few shallow constrictions parallel to the ribs. There are small tubercles at the umbilical edge, and the ribs are raised into small, blunt, elongated tubercles at the ventral shoulder. There are poorly preserved traces of mid-lateral tubercles on the smallest whorls.

DIMENSIONS. C.79240 – 67·0 : 30·5 (46%), 23·0 (34%), 18·5 (28%).

REMARKS. The figured specimen is probably closer to the specimen figured as var. *elegans* Spath (1939 : pl. XXI, figs 5a, b) than to the holotype of *S. uhligi* which has fewer ribs.

LOCALITY. Makerwal, Trans Indus Salt Ranges.

Sarasinella sp. indet.

MATERIAL. One fragment, C.79241.

HORIZON. 7 feet (2·1 m) below the top of the middle member of the Chichali Formation ; Valanginian (Lower).

REMARKS. This fragmentary specimen is recorded because of its stratigraphic importance. It differs from *S. uhligi* in having stronger ribs, a lower bifurcation point on the flank and more prominent constrictions. Both the umbilical and ventrolateral tubercles are also stronger. It appears to be close to *Sarasinella chichalensis* Spath (1939 : pl. XXI, figs 3, 4).

LOCALITY. Chichali Pass, Trans Indus Ranges.

Sarasinella cf. ***subspinosa*** (Uhlig 1910)

Pl. 11, fig. 7

1910 *Hoplites* (*Sarasinella*) *subspinosus* Uhlig : 239 ; pl. XC, figs 4a–c.

MATERIAL. One specimen, C.79242.

HORIZON. 8 to 10 feet (c. 2¾ m) below the top of the middle member of the Chichali Formation ; Valanginian (Lower).

REMARKS. This fragment differs from *S. uhligi* Spath in possessing prominent mid-lateral bullate tubercles on every third or fourth rib, and in being more evolute. The lateral tubercles appear to become weaker on the largest part of the specimen preserved, which has a diameter of about 55 mm. In these characters it agrees with *S. subspinosa*, and differs from the specimens of *S. uhligi* described above.

LOCALITY. Lunda Mines, Trans Indus Ranges.

Genus ***LEOPOLDIA*** Mayer-Eymar 1887

Leopoldia sp. indet.

Pl. 11, fig. 8

MATERIAL. Two specimens, C.79243–4.

HORIZON. Upper bed of the middle member of the Chichali Formation ; Valanginian (Upper).

DESCRIPTION. The larger of these two fragmentary specimens is wholly septate and 92 mm in diameter. The whorls are involute and compressed, and the convex flanks converge towards a narrow, tabulate venter. The ribs are weak or absent on most of the flank but they occur on the umbilical edge and are stronger on the ventral shoulder where they are prorsiradiate and swell into blunt tubercles. The middle of the venter is smooth. On the inner whorls the ventral tubercles are more prominent.

REMARKS. The specimen compares favourably with *L. leopoldi* (d'Orbigny) in its involute shell, whorl section and ornament, but differs in having less pronounced umbilical and ventral tubercles.

LOCALITIES. North-west of Malla Khel, Punnu Mines in the Trans Indus Ranges.

Genus ***NEOHOPLOCERAS*** Spath 1939

Neohoploceras baumbergeri Spath 1939

Pl. 12, fig. 3

1939 *Neohoploceras baumbergeri* Spath : 106 ; pl. XXII, figs 3a–b.
1962 *Neohoploceras besairiei* Collignon : pl. 192, fig. 875.

MATERIAL. Two specimens, C.79245–6.

HORIZON. 5 to 6 feet (c. $1\frac{2}{3}$ m) below the top of the middle member of the Chichali Formation ; Valanginian (Lower).

DESCRIPTION. Both specimens are 85 to 90 mm in diameter and wholly septate. The whorls are evolute and the whorl section is polygonal (hexagonal or octagonal), depressed, and has a tabulate and sulcate venter. The ribs are strong, rectiradiate on the flank, strongly projected over the ventral shoulder, and form forwardly-directed chevrons on the venter but are interrupted along the siphonal line. Every second or third rib bears a small umbilical tubercle, a large and prominent lateral tubercle and a weak swelling at the ventral shoulder. The intermediate ribs do not have umbilical or lateral tubercles but have slight swellings at the ventral shoulder. Some ribs bifurcate at the lateral tubercles. Constrictions are probably present on the inner whorl but are poorly preserved.

REMARKS. The figured specimen is similar in dimensions and other details to Spath's holotype. It is characterized by the forward projection of the ribs on the venter, lack of constrictions on the outer whorl and prominent thick bullae at the middle of the flank. Spath included the species in *Neohoploceras*, but the projection of the ribs on the venter and the lack of constrictions on the outer whorl is unlike the type species *Neohoploceras submartini* (Mallada) or the other *Neohoploceras* species Spath described (1939 : pl. XVII, figs 8a–c ; pl. XV, figs 10a–d ; pl. XXI, figs 8a–b) from the Trans Indus Ranges.

LOCALITY. South-west of Malla Khel, Trans Indus Ranges.

Neohoploceras submartini (Mallada 1882)

Pl. 11, fig. 6

1882 *Ammonites submartini* Mallada : pl. X, figs 7–9 ; pl. XI, figs 12–14.
1939 *Neohoploceras submartini* (Mallada) Spath : 105 ; pl. XVI, figs 1a–d (with synonymy).
1962 *Neohoploceras submartini* (Mallada) ; Collignon : pl. 192, fig. 872.

MATERIAL. One complete specimen, C.79247, and one fragment, C.79248.

HORIZON. 4 to 5 feet (c. 1⅓ m) below the top of the middle member of the Chichali Formation ; Valanginian (Lower).

DESCRIPTION. The complete specimen is involute, moderately inflated and wholly septate. The flanks are arched and the venter is fairly narrow and grooved. Three constrictions parallel to the ribs and bordered on the umbilical shoulder by stronger tubercles are present on the outer whorl.

The ribs are fairly strong and rectiradiate, and they commonly bifurcate from prominent umbilical tubercles and bifurcate again at about the middle of the flank. Occasional ribs do not have umbilical tubercles and either remain simple or bifurcate at the middle of the flank. All the ribs terminate on the ventral shoulder in small incipient tubercles. There are four constrictions on the outer whorl, parallel to the ribs, and the rib behind each one has a much larger tubercle on the ventral shoulder.

DIMENSIONS. C.79247 – 46·5 : 21·0 (45%), 19·0 (41%), 11·0 (24%).

REMARKS. The figured specimen compares well in ribbing and constrictions with Spath's (1939) and Collignon's (1962) figures, except that the mid-lateral tubercles are not developed.

LOCALITY. Makerwal, Trans Indus Ranges.

Neohoploceras collignoni sp. nov.

Pl. 12, fig. 1

DIAGNOSIS. Moderately large evolute form, with a polygonal whorl section and a tabulate to sulcate venter ; mid-lateral and ventral bullate tubercles, strong ribs that commonly bifurcate from the middle of flank, but occasionally remain simple, and some intercalated ribs ; deep constrictions.

HOLOTYPE. C.79249, the only specimen.

STRATIGRAPHIC RANGE. Upper part of middle member of the Chichali Formation; Valanginian (Upper).

DESCRIPTION. The inner whorls are depressed and have a grooved venter. They have ribs that become thick and have flat tops on the upper half of the flanks and the ventral shoulder where they terminate in square-topped bullae. Lateral bullae also occur near the middle of the flank and prominent deep constrictions are present. Half of the outer whorl is body-chamber which is massive, but more compressed than the inner whorl. The ribs are strong, fairly widely spread and either simple or bifurcate at the middle of the flank, and there are many intercalated ribs. The lateral tubercles are much smaller than on the inner whorl but the bullae bordering the sulcate venter remain strong and are present on every rib. There is a tendency for blunt tubercles to develop at the umbilical edge. Deep constrictions are present on the outer whorl.

DIMENSIONS. C.79249 – 167·0 : 60·0 (36%), 61·0 (37%), 62·0 (37%).

REMARKS. The new species may be distinguished from other species of the genus by its large size, whorl shape, irregular thick and flat-topped ribs, and prominent lateral and ventral tubercles.

LOCALITY. South-west of Malla Khel, Trans Indus Ranges.

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Wright, C. W. 1957. *see* Arkell, Kummel & Wright.

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PLATE 1

All figures natural size

Neolissoceras grasianum (d'Orbigny) (p. 263)

Figs 1a, 1b.	Berriasian. Malla Khel, Trans Indus Range. C.79101.
Figs 2a, 2b.	Berriasian. Punnu Mines, Trans Indus Range. C.79102.

Spiticeras (Spiticeras) mojsvari (Uhlig) (p. 264)

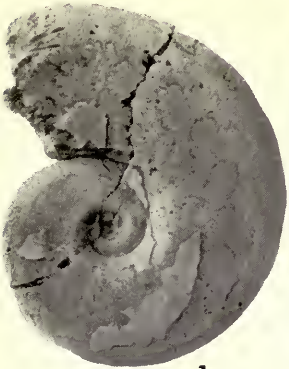
Figs 3a, 3b.	Berriasian. Khadimakh (south flank), Kohat district. C.79107.

Spiticeras (Spiticeras) cf. ***griesbachi*** (Uhlig) (p. 264)

Figs 4a, 4b.	Berriasian. South of Fort Lockhart, Samana Range. C.79106.

Olcostephanus (Olcostephanus) salinarius Spath
(p. 266; see also Pl. 2, fig. 4 and Pl. 3, fig. 1)

Figs 5a, 5b.	Valanginian. Lunda Mines, Trans Indus Range. C.79117.
Figs 6a, 6b.	Valanginian. Chichali Pass, Trans Indus Range. C.79111.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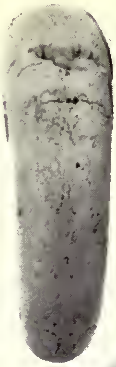
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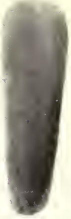
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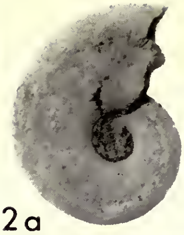
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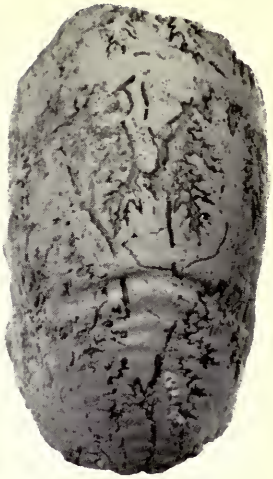
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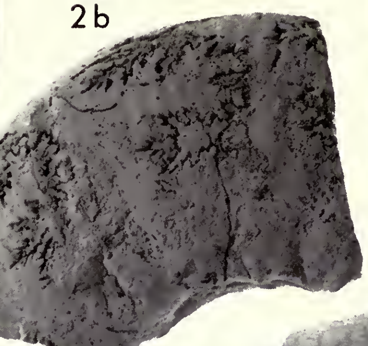
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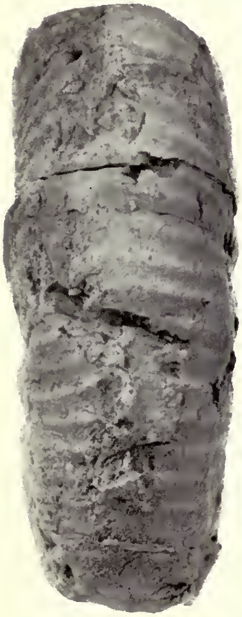
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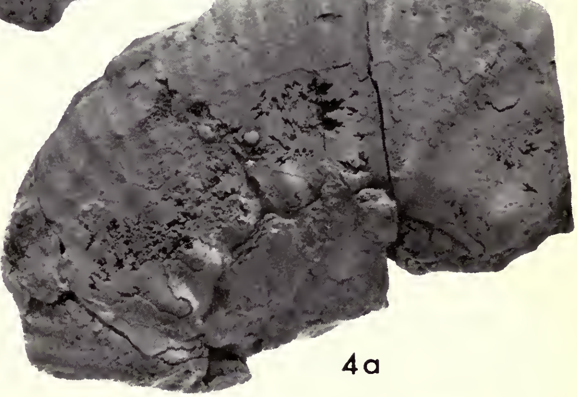
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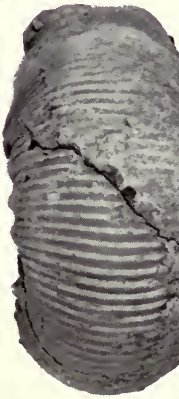
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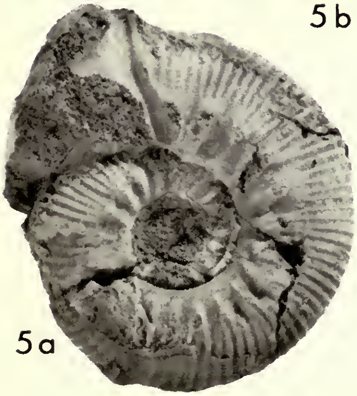
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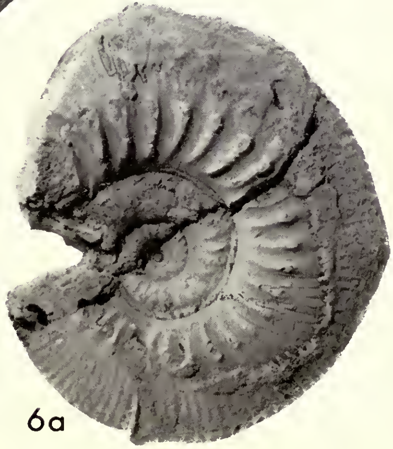
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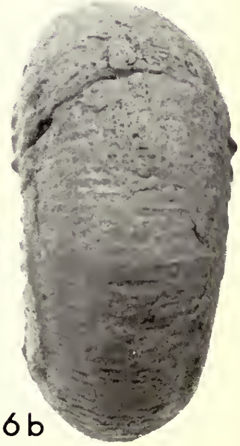
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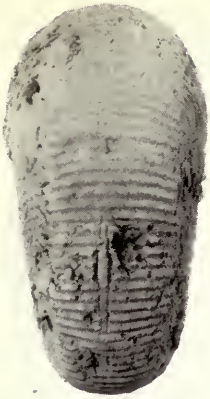
PLATE 2

Olcostephanus (Olcostephanus) sakalavensis (Besairie)
(p. 267 ; see also Pl. 3, fig. 2 and Pl. 4, fig. 3)
Figs 1a, 1b. U. Valanginian. Chichali Pass, Trans Indus Range. C.79126, × 1·0.
Figs 3a, 3b. U. Valanginian. Khadimakh, Kohat district. C.79131, × 1·0.

Spiticeras (Negreliceras) tenuicostatum Djanélidzé (p. 265)
Figs 2a, 2b. Berriasian. SW of Malla Khel, Trans Indus Range. C.79108, × 0·6.

Olcostephanus (Olcostephanus) salinarius Spath
(p. 266 ; see also Pl. 1, figs 5, 6 and Pl. 3, fig. 1)
Figs 4a, 4b. Valanginian. Makerwal, Trans Indus Range. C.79120, × 1·0.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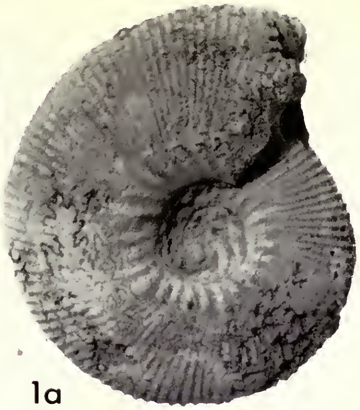
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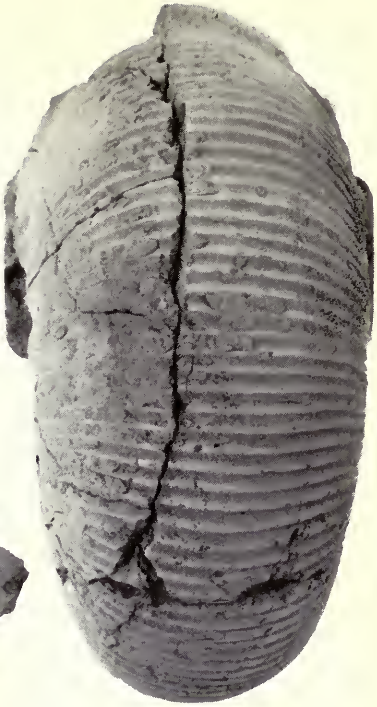
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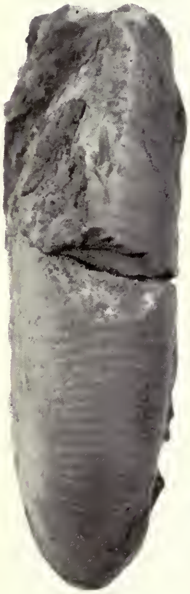
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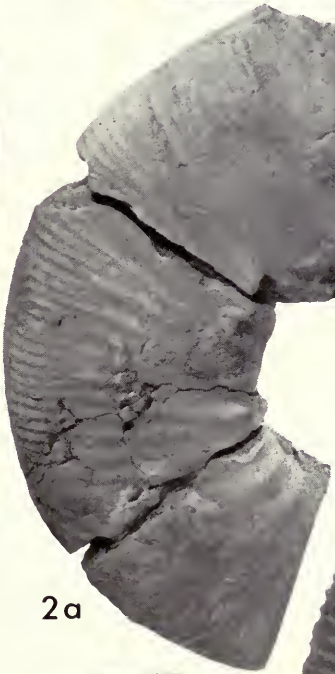
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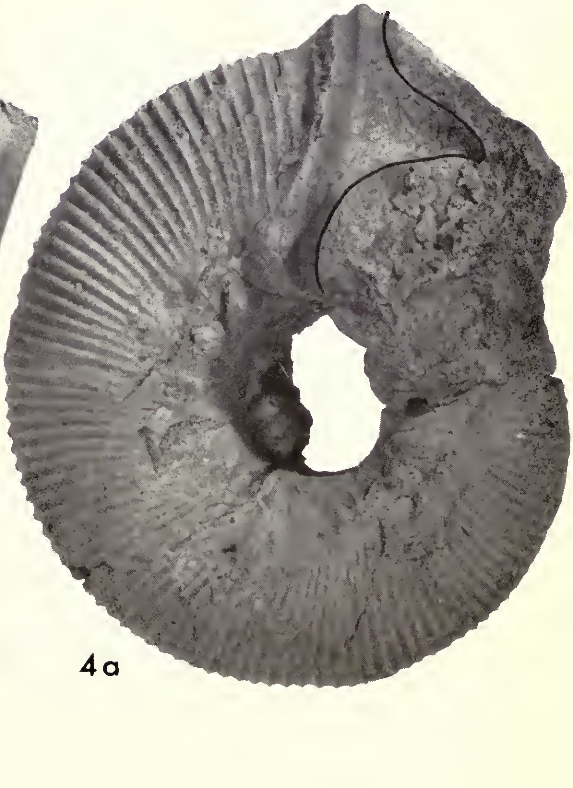
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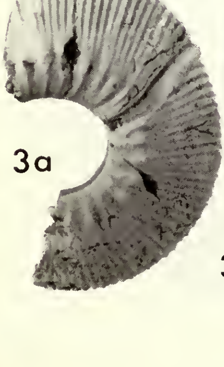
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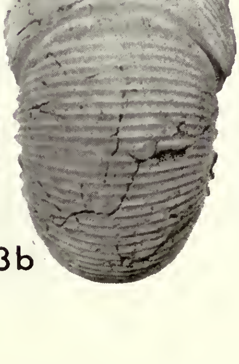
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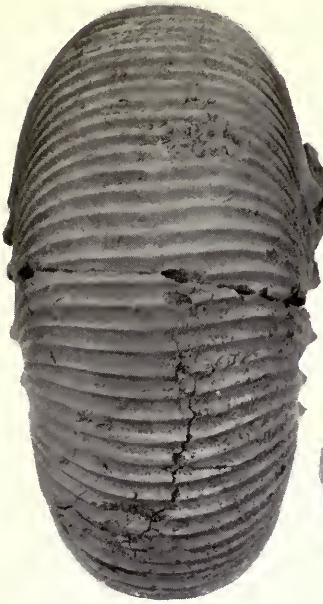
PLATE 3

All figures natural size

Olcostephanus (Olcostephanus) salinarius Spath
(p. 266 ; see also Pl. 1, figs 5, 6 and Pl. 2, fig. 4)
Figs 1a, 1b. Valanginian. Malla Khel, Trans Indus Range. C.79118.

Olcostephanus (Olcostephanus) sakalavensis (Besairie)
(p. 267 ; see also Pl. 2, figs 1, 2 and Pl. 4, fig. 3)
Figs 2a, 2b. U. Valanginian. Makerwal, Trans Indus Range. C.79132.

Olcostephanus (Olcostephanus) fascigerus Spath (p. 268)
Figs 3a, 3b. U. Valanginian. Makerwal, Trans Indus Range. C.79136.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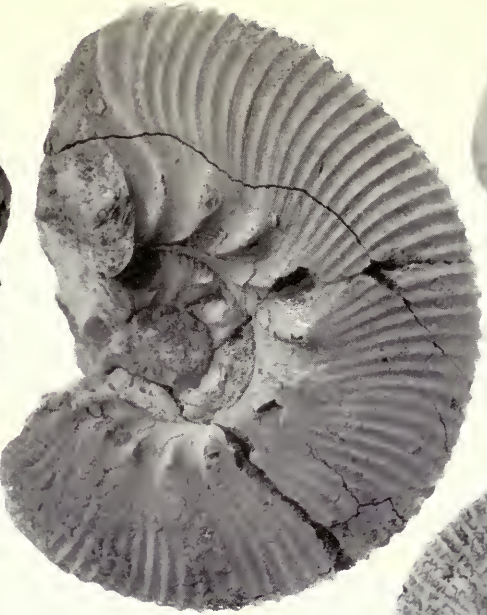
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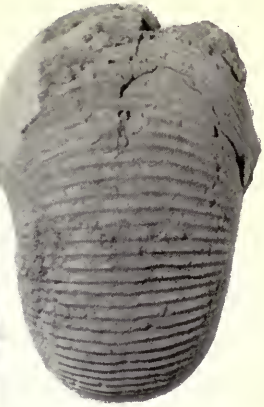
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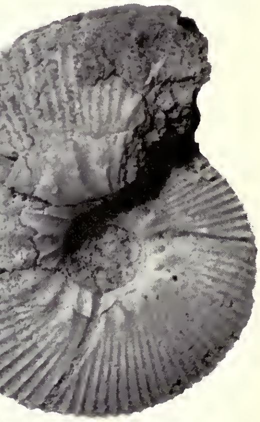
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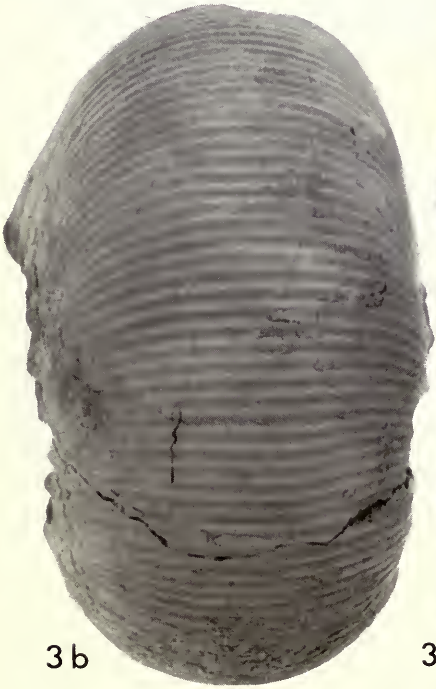
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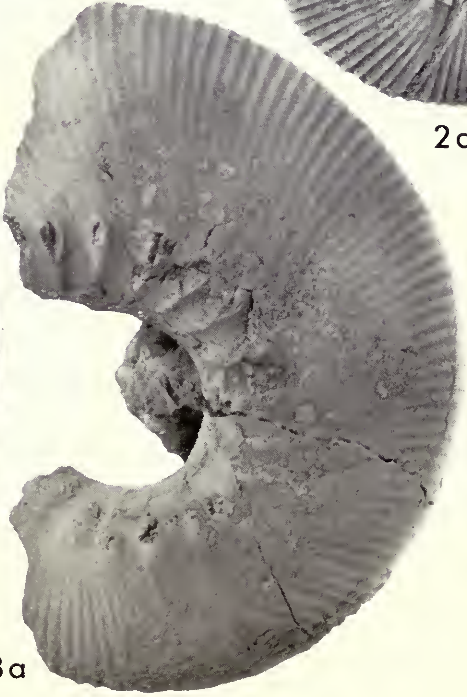

3a

PLATE 4

Olcostephanus (Olcostephanus) globosus Spath (p. 270)

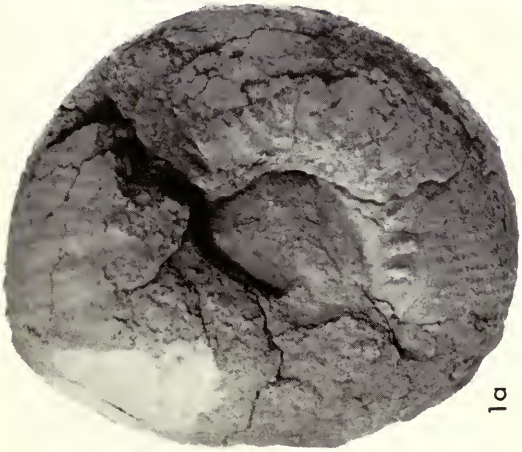
Figs 1a, 1b. U. Valanginian. Chichali Pass, Trans Indus Range. C.79143, × 0·8.

Olcostephanus (Olcostephanus) sublaevis Spath (p. 269)

Figs 2a, 2b. U. Valanginian. Punnu Mines, Trans Indus Range. C.79137, × 0·58.

Olcostephanus (Olcostephanus) sakalavensis (Besairie)
(p. 267 ; see also Pl. 2, figs 1, 3 and Pl. 3, fig. 2)

Figs 3a, 3b. U. Valanginian. SW of Malla Khel, Trans Indus Range. C.79127, × 0·8.



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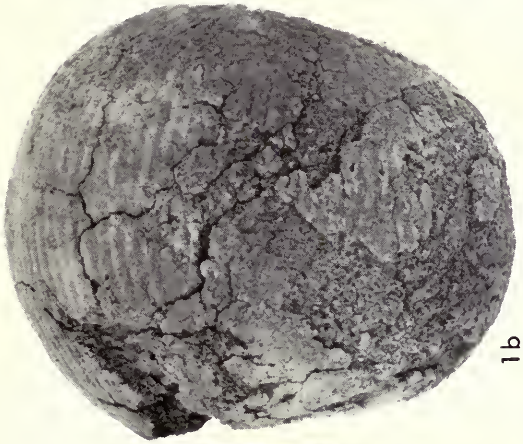

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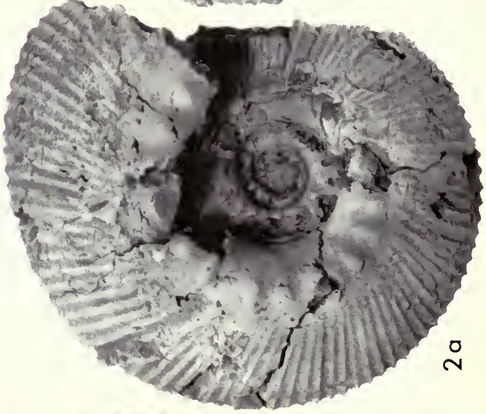

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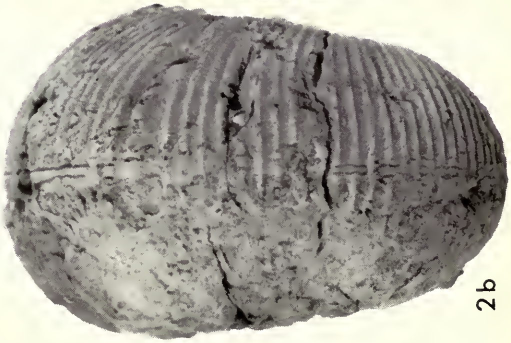

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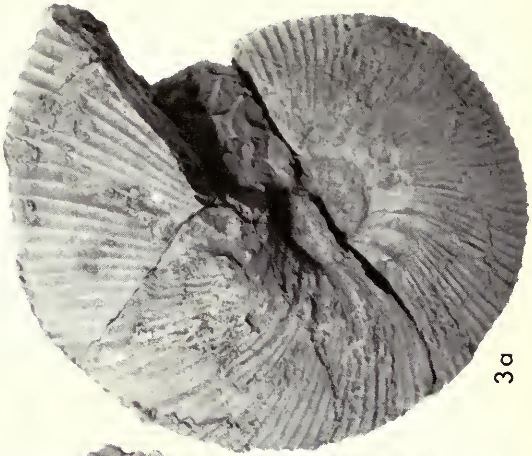

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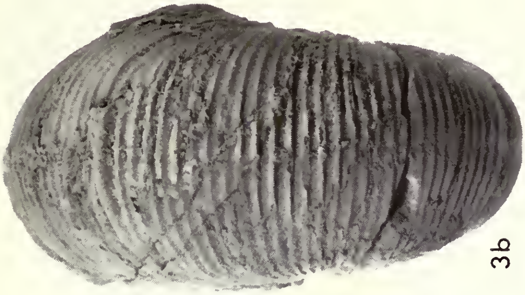


3b

PLATE 5

All figures natural size

Olcostephanus (Rogersites) schenki (Oppel) (p. 270)

FIGS 1a, 1b. U. Valanginian. Punnu Mines, Trans Indus Range. C.79146.

Berriasella sp. indet. (p. 272)

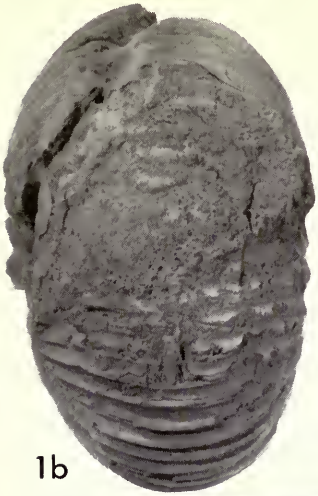
FIGS 2a, 2b. Berriasian. SW of Malla Khel, Trans Indus Range. C.79151.

Olcostephanus (Rogersites) madagascariensis Lemoine
var. ***isakhelensis*** nov. (p. 272)

FIGS 3a, 3b. U. Valanginian. Lunda Mines, Trans Indus Range. C.79148.

Olcostephanus (Rogersites) madagascariensis Lemoine (p. 271)

FIGS 4a, 4b. U. Valanginian. Lunda Mines, Trans Indus Range. C.79147.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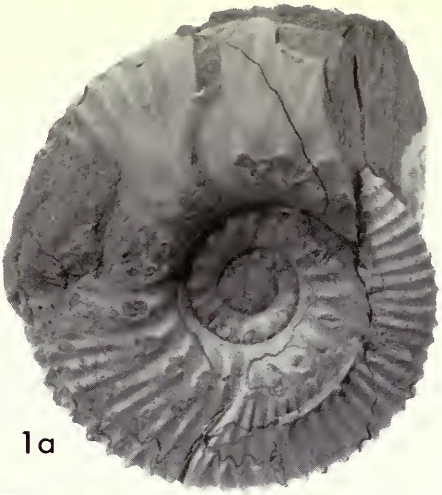
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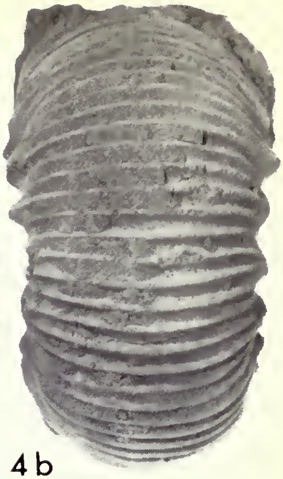
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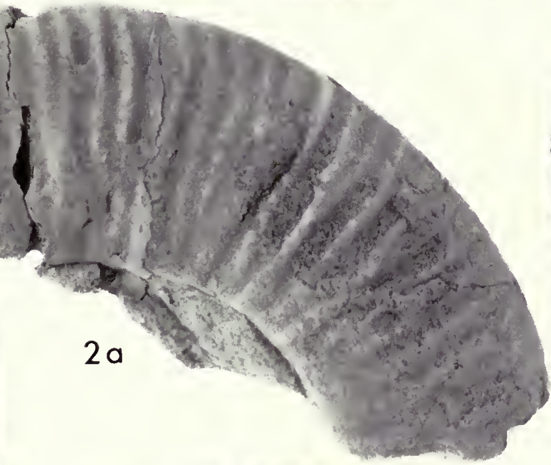
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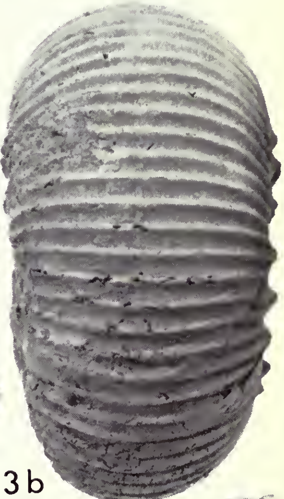
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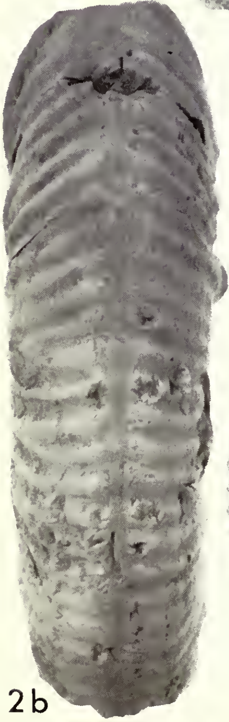
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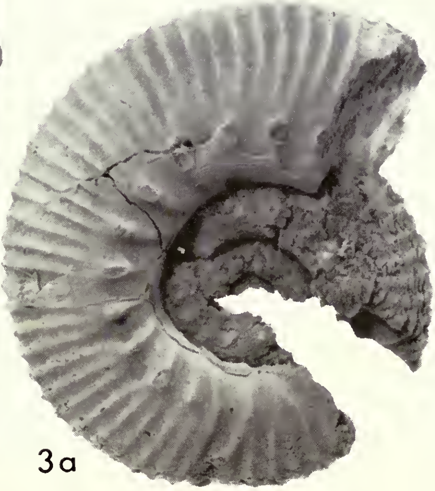
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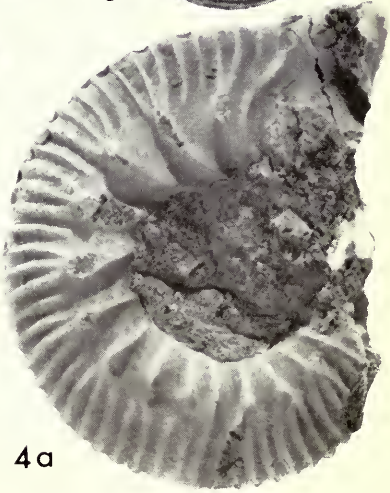
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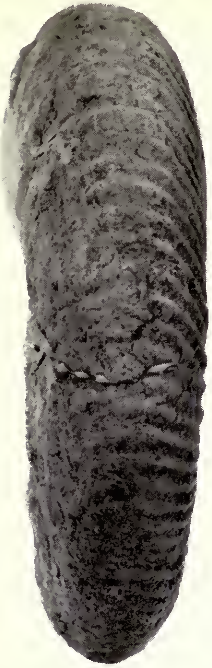
PLATE 6

Subthurmannia fermori Spath (p. 273 ; see also Pl. 7, fig. 1)

FIGS 1a, 1b ; 3a, 3b. Berriasian. Chichali Pass, Trans Indus Range. Figs 1, C.79152, × 0·75. Figs 3, C.79154, × 1·0.

Subthurmannia filosa Spath (p. 274 ; see also Pl. 7, fig. 3)

FIGS 2a, 2b. Berriasian. Chichali Pass, Trans Indus Range. C.79160, × 1·0.



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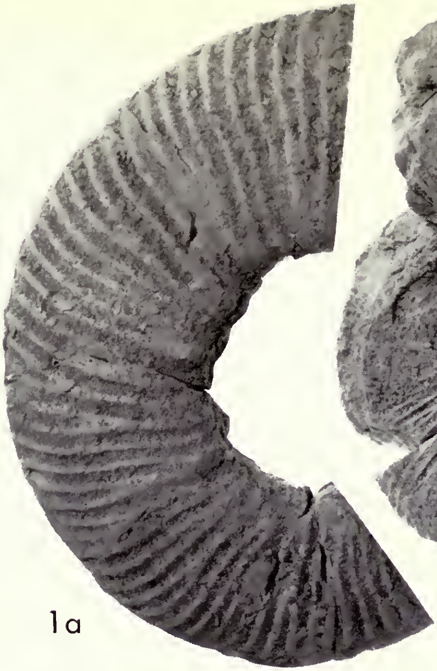

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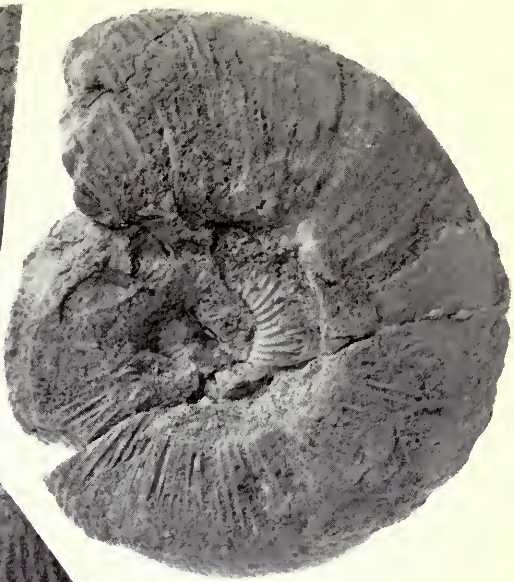

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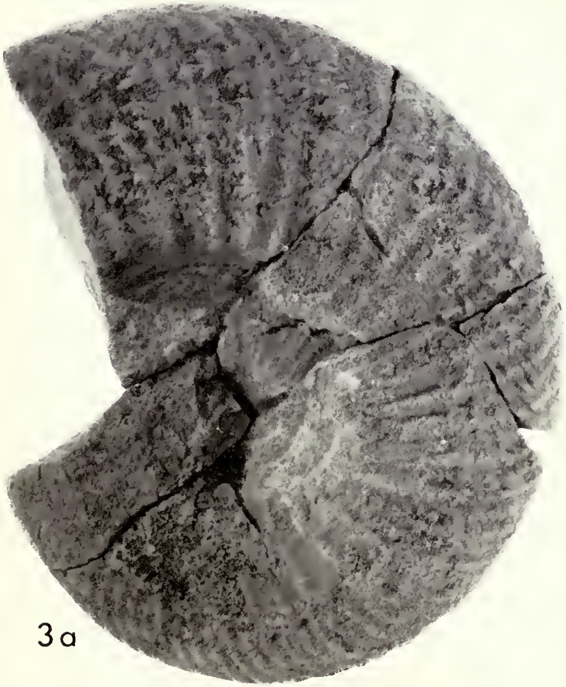

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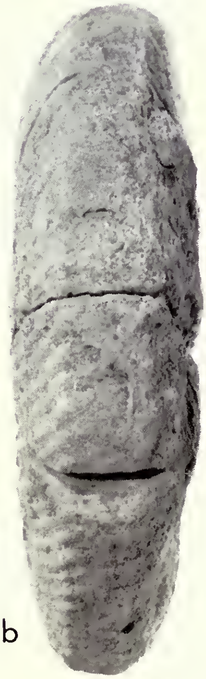

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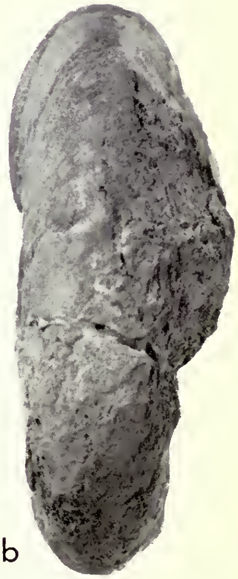


2b

PLATE 7

Subthurmannia fermori Spath var. ***surgharensis*** nov.
(p. 273 ; see also Pl. 6, fig. 1)

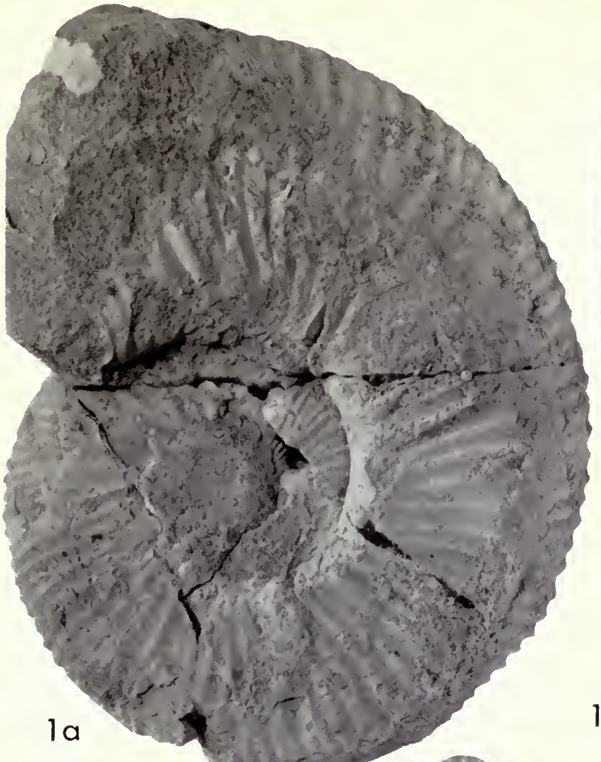
FIGS 1a, 1b. Berriasian. SW of Malla Khel, Trans Indus Range. C.79157, × 1·0.

Subthurmannia transitoria Spath (p. 275 ; see also Pl. 10, fig. 4)

FIGS 2a, 2b. Berriasian. Chichali Pass, Trans Indus Range. C.79163, × 0·6.

Subthurmannia filosa Spath (p. 274 ; see also Pl. 6, fig. 2)

FIGS 3a, 3b. Berriasian. Chichali Pass, Trans Indus Range. C.79162, × 1·0.



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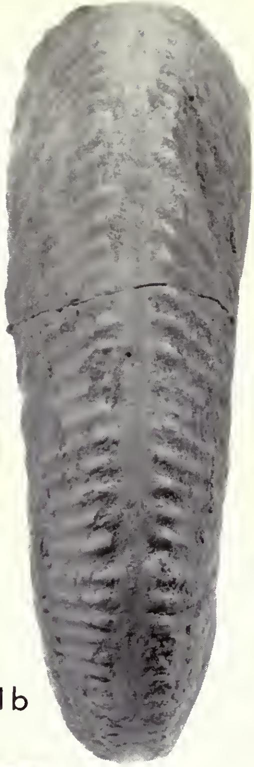

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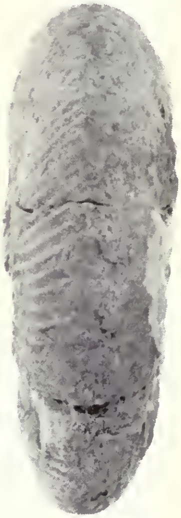

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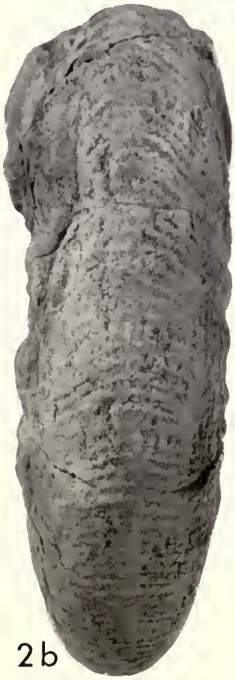

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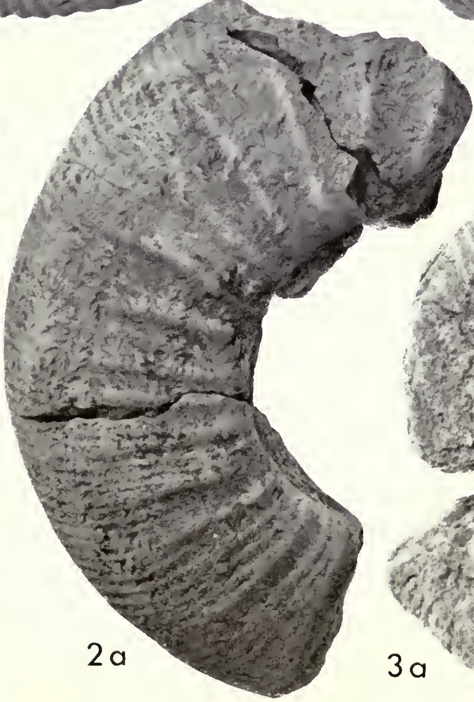

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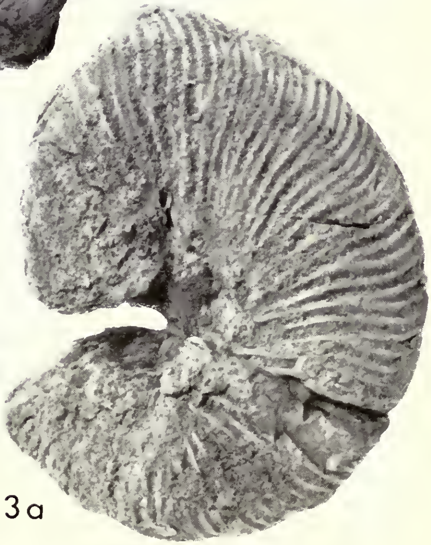


3a

PLATE 8

Neocomites (Neocomites) copei sp. nov. (p. 278)

Figs 1a, 1b. L. Valanginian. Lunda Mines, Trans Indus Range. C.79186, holotype, × 1·0.

Neocomites (Neocomites) pycnoptychus (Uhlig) (p. 280)

Figs 2a, 2b. L. Valanginian. SW of Malla Khel, Trans Indus Range. C.79193, × 1·0.

Neocomites (Neocomites) campylotoxus (Uhlig) (p. 279)

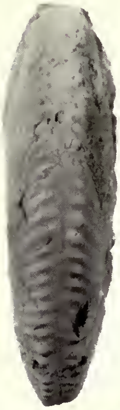
Fig. 3. L. Valanginian. Chichali Pass, Trans Indus Range. C.79190, × 1·0.
Fig. 4. L. Valanginian. Khadimakh, Kohat district. C.79191, × 1·0.

Neocomites (Neocomites) similis Spath (p. 280 ; see also Pl. 9, figs 1, 3)

Figs 5a, 5b, 7a, 7b. L. Valanginian. Chichali Pass, Trans Indus Range. Figs 5, C.79196, × 1·0. Figs 7, C.79198, × 1·0.

Protacanthodiscus asiaticus (Uhlig) (p. 276)

Figs 6a, 6b. Berriasian. Chichali Pass, Trans Indus Range. C.79178, × 0·7.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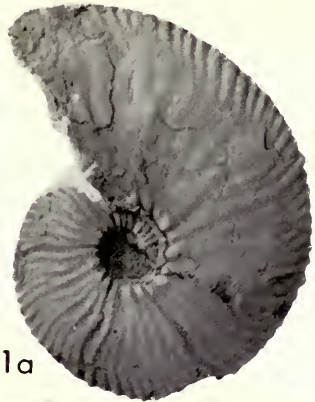
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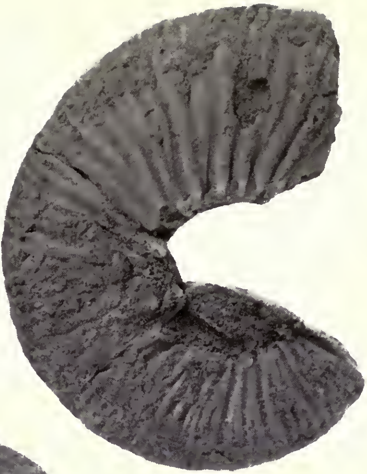
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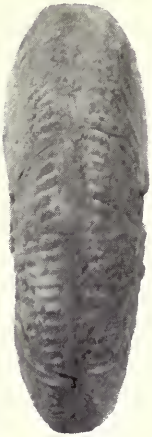
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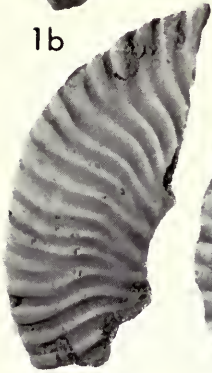
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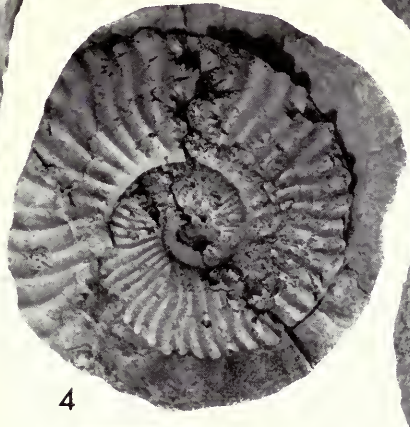
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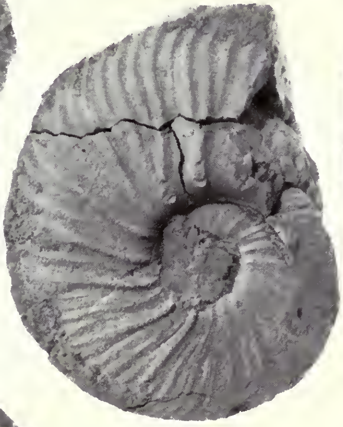
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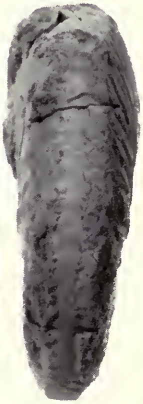
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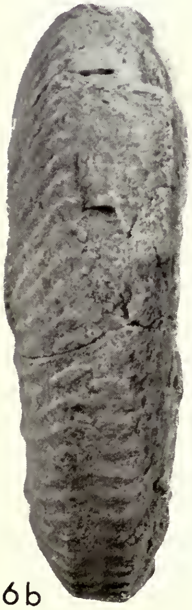
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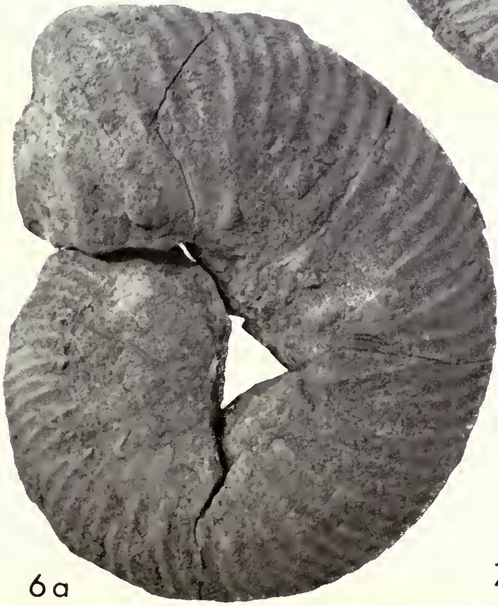
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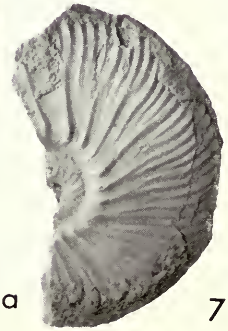

7a

7b

PLATE 9

All figures natural size

Neocomites (Neocomites) similis Spath (p. 280 ; see also Pl. 8, figs 5, 7)

Figs 1a, 1b, 3a, 3b. L. Valanginian. Chichali Pass, Trans Indus Range. Figs 1, C.79197. Figs 3, C.79203.

Neocomites (Parandiceras) rota Spath (p. 282)

Figs 2a, 2b. L. Valanginian. SW of Malla Khel, Trans Indus Range. C.79208.

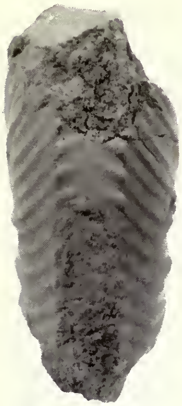
Figs 5a, 5b. L. Valanginian. Makerwal, Trans Indus Range. C.79209.

Neocomites (Neocomites) trezanensis Sayn (p. 281)

Figs 4a, 4b. L. Valanginian. Punnu Mines, Trans Indus Range. C.79206.

Lyticoceras (Besairieceras) colcanapi (Collignon) (p. 283 ; see also Pl. 10, fig. 3)

Figs. 6a, 6b. U. Valanginian. Lunda Mines, Trans Indus Range. C.79216.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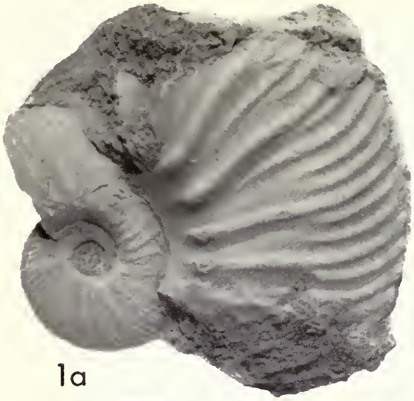
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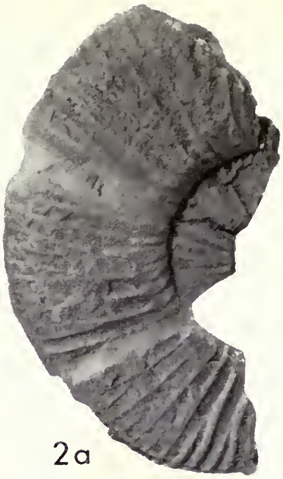
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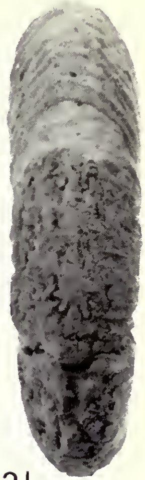
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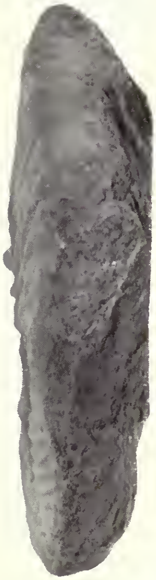
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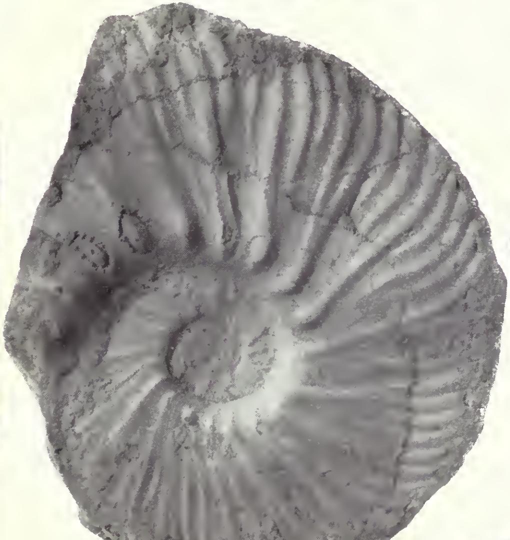
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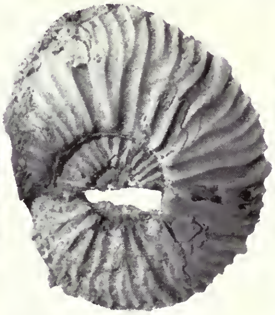
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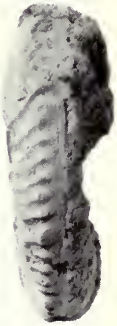
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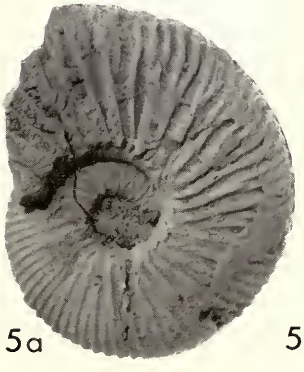
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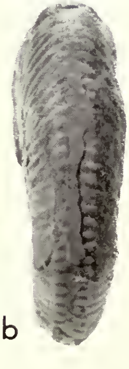
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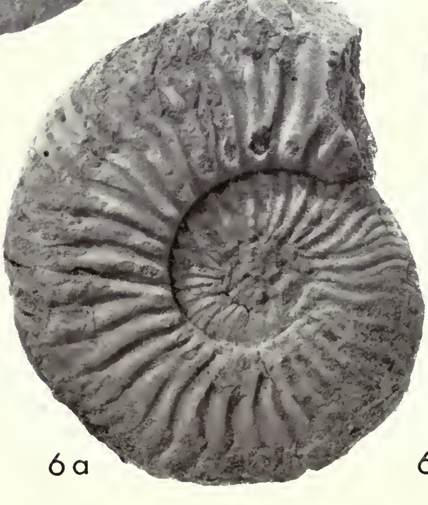
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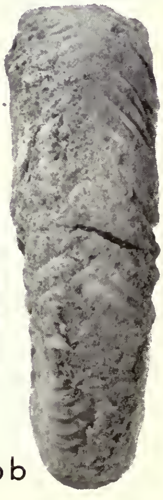

6b

PLATE 10

All figures × 0·7

Thurmanniceras sp. indet. 1 (p. 277)

Figs 1a, 1b. L. Valanginian. SW of Malla Khel, Trans Indus Range. C.79179.

Neocosmoceras octagonum (Blanford) (p. 288)

Figs 2a, 2b. Berriasian. South of Fort Lockhart, Samana Range, Western Kohat. C.79222.

Lyticoceras (Besairieceras) colcanapi (Collignon)
(p. 283; see also Pl. 9, fig. 6)

Figs 3a, 3b. U. Valanginian. Malla Khel, Trans Indus Range. C.79214.

Subthurmannia transitoria Spath var. ***noori*** nov.
(p. 275; see also Pl. 7, fig. 2)

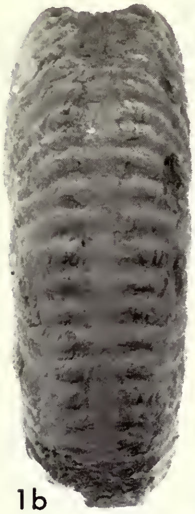
Figs 4a, 4b. Berriasian. Chichali Pass, Trans Indus Range. C.79165.

Lyticoceras (Besairieceras) planecostatum (Collignon) (p. 284)

Figs 5a, 5b. U. Valanginian. Malla Khel, Trans Indus Range. C.79220.

? Neocosmoceras subradiatum (Uhlig) (p. 286)

Figs 6a, 6b. Berriasian. Punnu Mines, Trans Indus Range. C.79225.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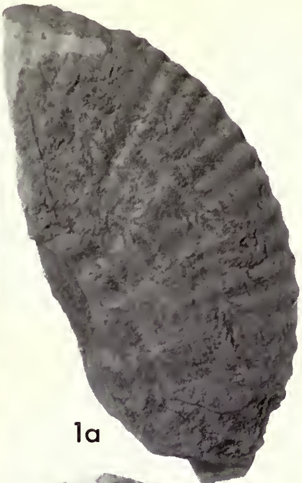
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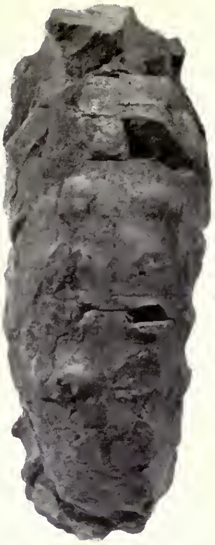
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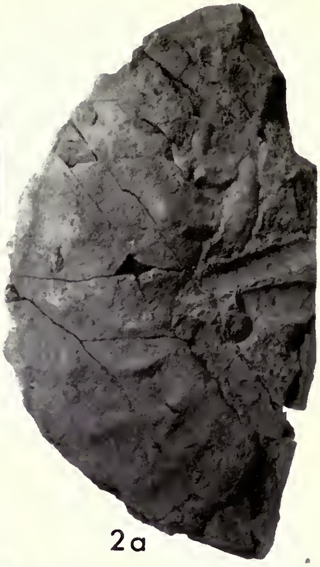
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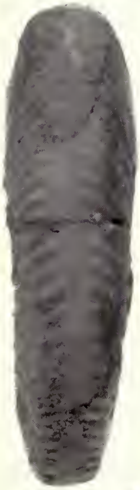
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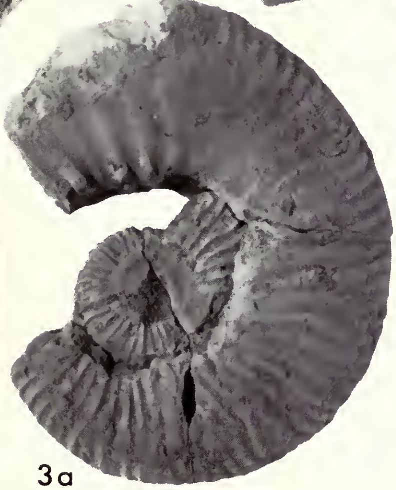
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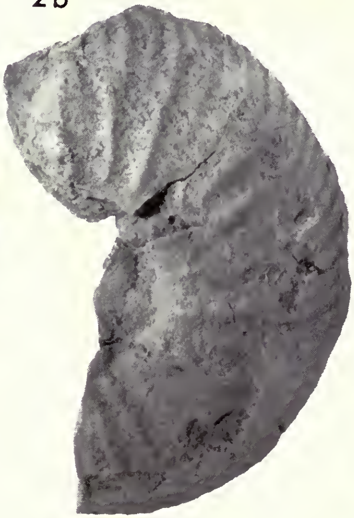
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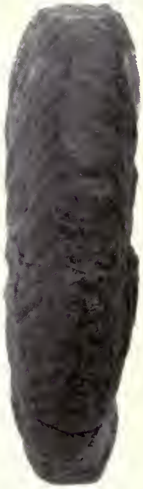
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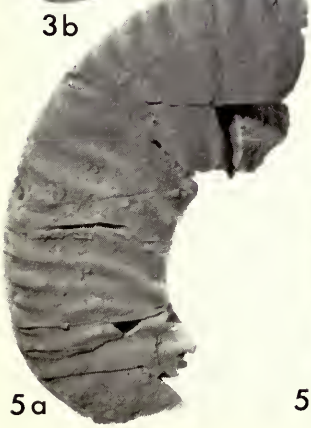
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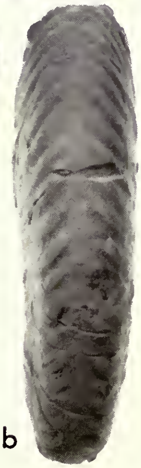
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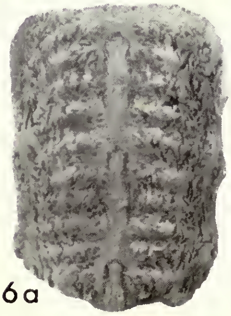
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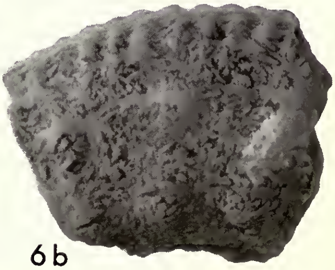

6b

PLATE 11

All figures natural size

Kilianella asiatica Spath (p. 286)

Figs 1a, 1b, 5a, 5b. L. Valanginian. Chichali Pass, Trans Indus Range. Figs 1, C.79228. Figs 5, C.79232.

Distoloceras sp. indet. (p. 288)

Figs 2a, 2b. L. Valanginian. SW of Malla Khel, Trans Indus Range. C.79235.

Figs 4a, 4b. U. Valanginian. SW of Malla Khel, Trans Indus Range. C.79236.

Kilianella cf. ***besairiei*** Spath (p. 287)

Figs 3a, 3b. L. Valanginian. Chichali Pass, Trans Indus Range. C.79233.

Neohoploceras submartini (Mallada) (p. 291)

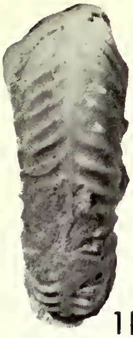
Figs 6a, 6b. L. Valanginian. Makerwal, Trans Indus Range. C.79247.

Sarasinella cf. ***subspinosa*** (Uhlig) (p. 289)

Figs 7a, 7b. L. Valanginian. Lunda Mines, Trans Indus Range. C.79242.

Leopoldia sp. indet. (p. 290)

Figs 8a, 8b. U. Valanginian. NW of Malla Khel, Trans Indus Range. C.79243.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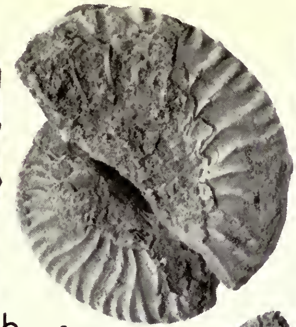
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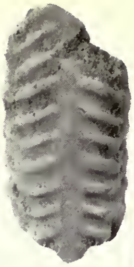
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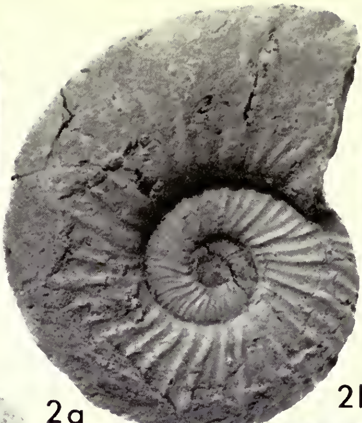
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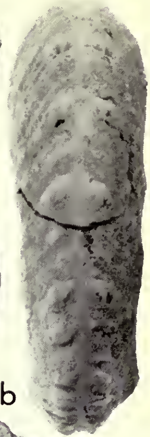
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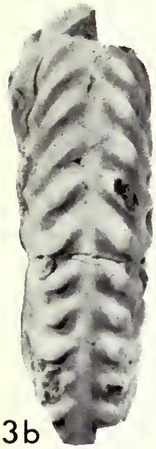
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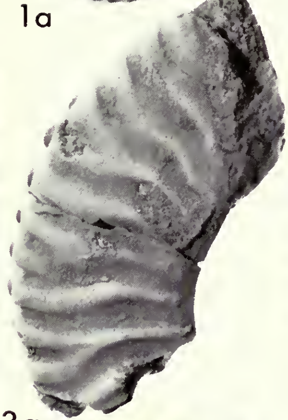
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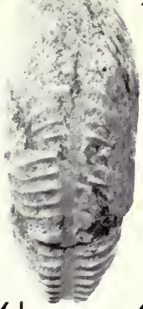
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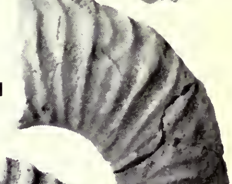
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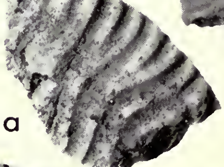
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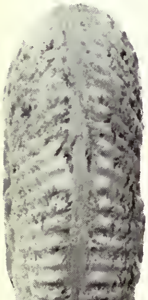
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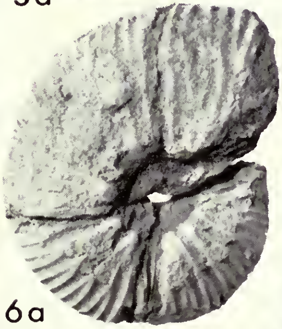
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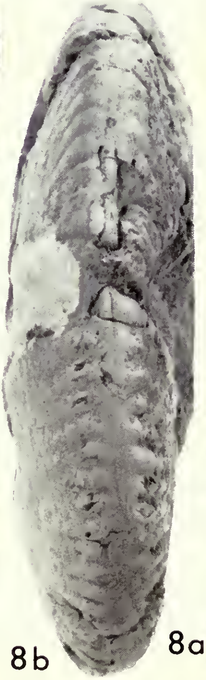
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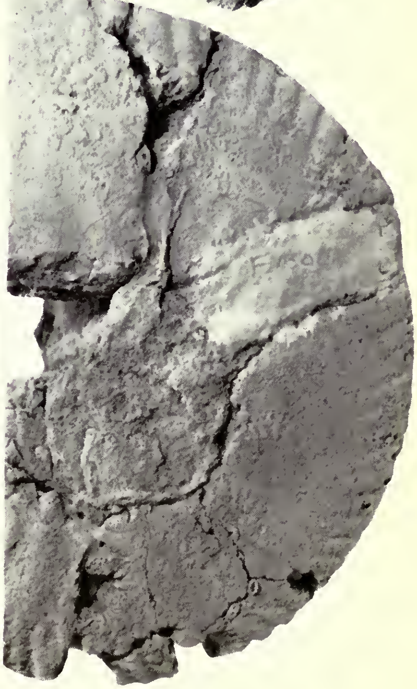
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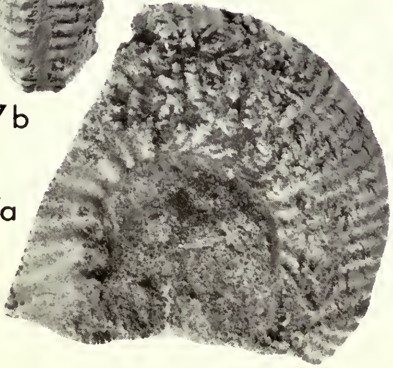

7a

PLATE 12

Neohoploceras collignoni sp. nov. (p. 291)

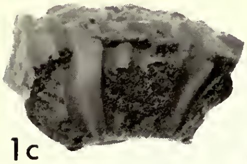
FIGS 1a, 1b, 1c, 1d. U. Valanginian. SW of Malla Khel, Trans Indus Range. C.79249, holotype. Figs 1a, 1b, ×0·6. Figs 1c, 1d, ×1·0.

Sarasinella uhligi Spath (p. 288)

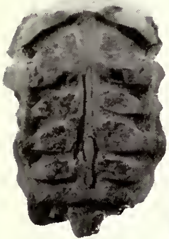
FIGS 2a, 2b. L. Valanginian. Makerwal, Trans Indus Range. C.79240, ×1·0.

Neohoploceras baumbergeri Spath (p. 290)

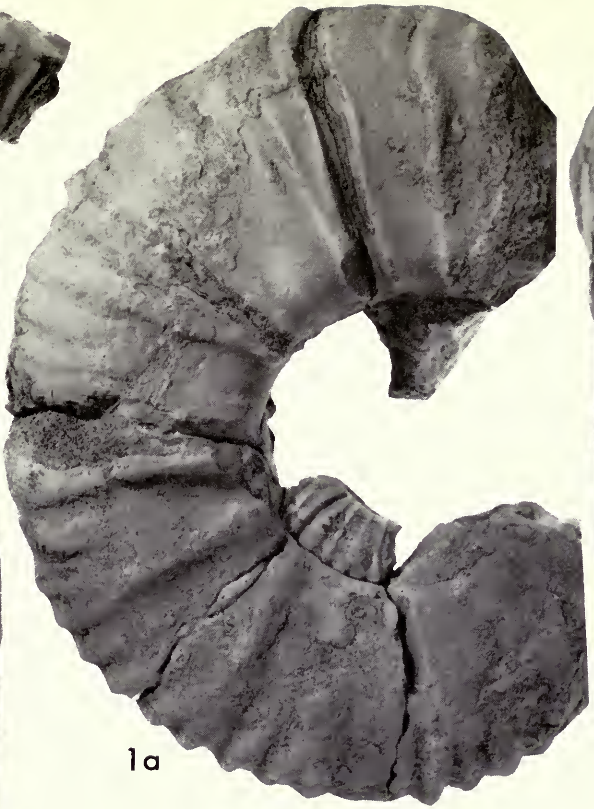
FIGS 3a, 3b. L. Valanginian. SW of Malla Khel, Trans Indus Range. C.79245, ×1·0.



1c



1d



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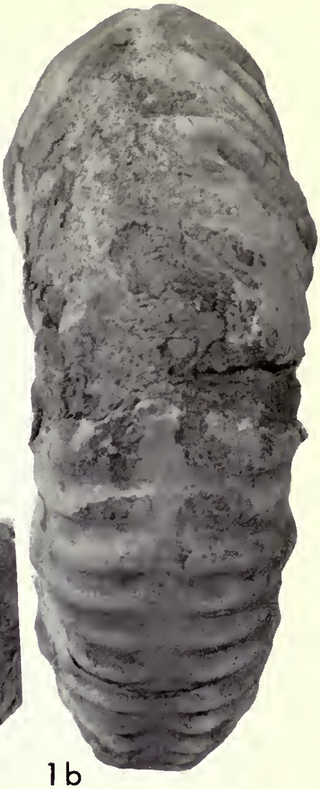

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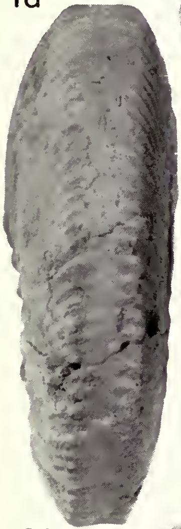

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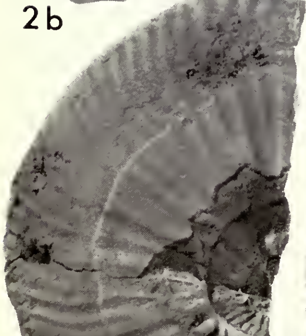

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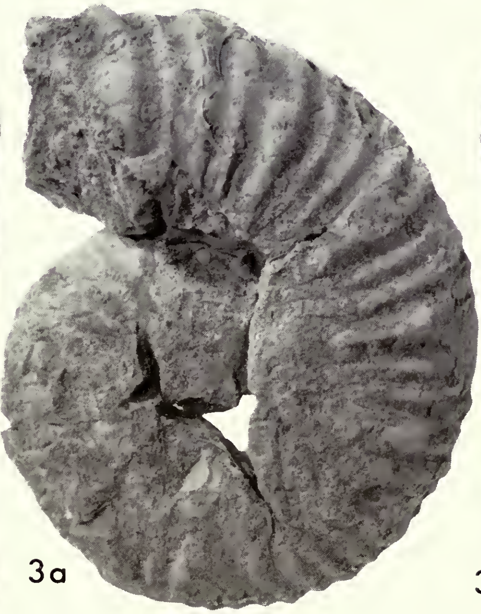

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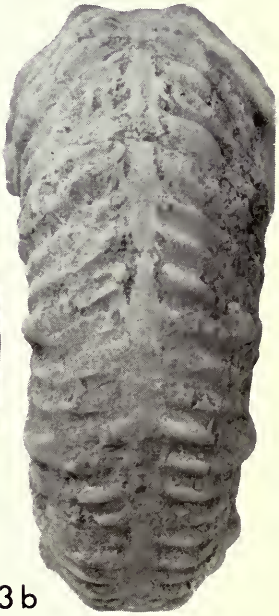

3b

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